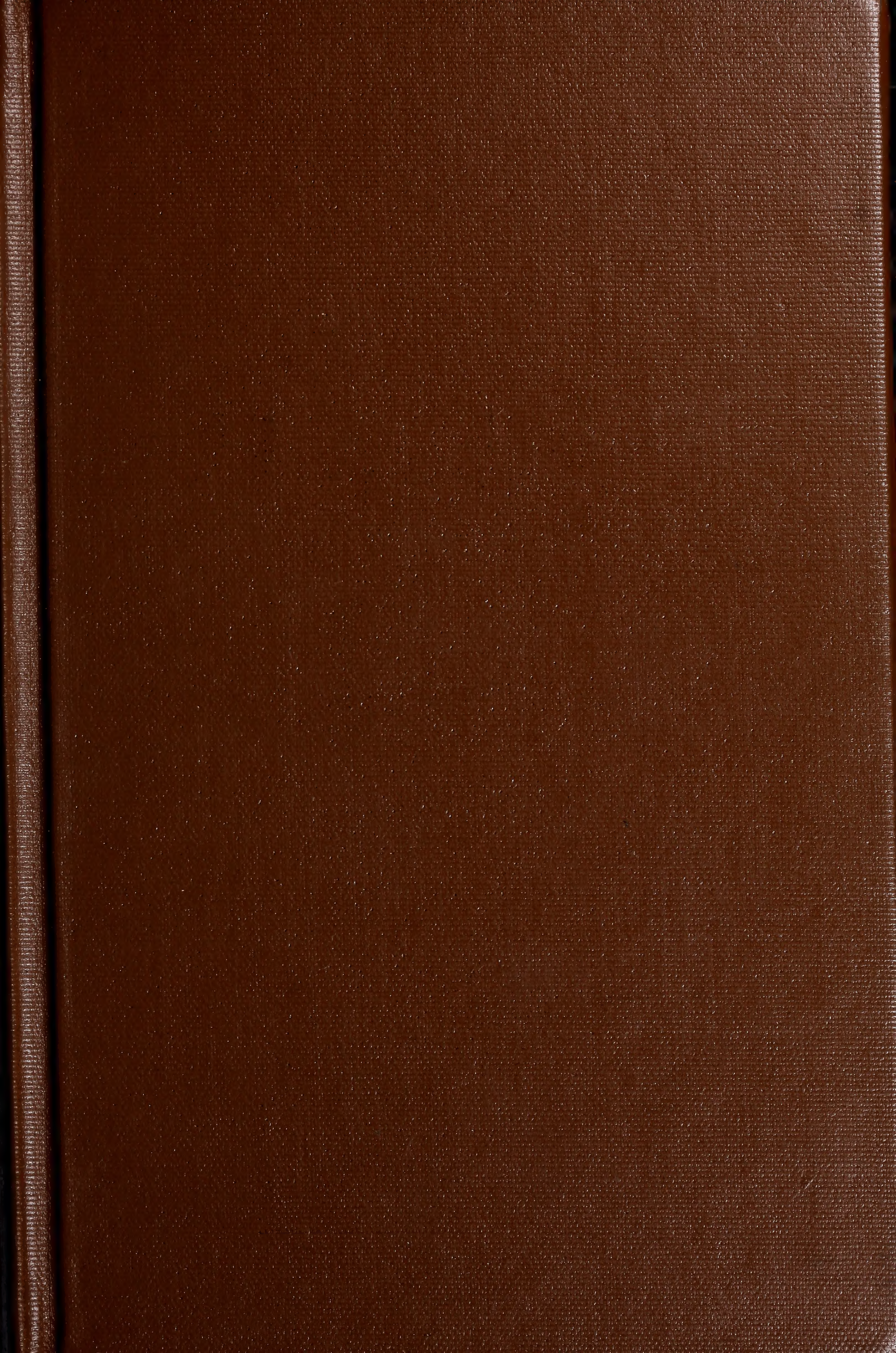



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Die Zeitschrift für Säugetierkunde veröffentlicht Originalarbeiten und wissenschaftliche Kurzmitteilungen aus dem Gesamtgebiet der Säugetierkunde, Besprechungen der wichtigsten internationalen Literatur sowie die Bekanntmachungen der Deutschen Gesellschaft für Säugetierkunde. Verantwortlicher Schriftleiter im Sinne des Hamburgischen Pressegesetzes ist Prof. Dr. Dieter Kruska.

Zusätzlich erscheint einmal im Jahr ein Heft mit den Abstracts der Vorträge, die auf der jeweiligen Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde gehalten werden. Sie werden als Supplement dem betreffenden Jahrgang der Zeitschrift zugeordnet. Verantwortlich für ihren Inhalt sind ausschließlich die Autoren der Abstracts.

Manuskripte: Manuskriptsendungen sind zu richten an die Schriftleitung, z. Hd. Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Biologie-Zentrum, Neue Universität, Olshausenstr. 40–60, W-2300 Kiel, Bundesrepublik Deutschland. Für die Publikation vorgesehene Manuskripte sollen gemäß den „Redaktionellen Richtlinien" abgefaßt werden. In ihnen finden sich weitere Hinweise zur Annahme von Manuskripten, Bedingungen für die Veröffentlichung und die Drucklegung, ferner Richtlinien für die Abfassung eines Abstracts und eine Korrekturzeichentabelle. Die Richtlinien sind auf Anfrage bei der Schriftleitung und dem Verlag erhältlich.

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A parapatric scenery: the distribution and ecology of *Sorex araneus* and *S. coronatus* (Insectivora, Soricidae) in southwestern Germany

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Abstract

Studied the distribution of *Sorex araneus* and *S. coronatus* in southwestern Germany along a transect from the Upper Rhine Valley to the highest elevation, the Feldberg, in the Black Forest. The species were determined by polyacrylamide gel electrophoresis of total blood proteins. In the study area, the two species occurred in parapatry and showed an alternating altitude distributional pattern.

S. araneus was found in the bottom of the Upper Rhine Valley and in the heights of the Feldberg, while *S. coronatus* was present in the lower and intermediate altitude levels of the Black Forest. In the Zastler Valley, *S. coronatus* advances 400 m farther uphill than in the St. Wilhelmer Valley where the climate is relatively cold and inclement. Two contact zones were found, situated at different altitudes according to the valley. In the study area, the species appeared to be altitudinal vicariads.

The ecology and distributional history of *S. araneus* and *S. coronatus* are discussed in comparison with available data on their respective areas of distribution. It is argued that *S. araneus* occupies regions with rather continental climatic characters either on dry or wet soils. On the other hand, *S. coronatus* prefers Atlantic climates and balanced soil humidity. The competitive interaction between *S. coronatus* and *S. araneus* and its biogeographical consequences are discussed.

Introduction

During the last 40 years, it gradually became obvious that in central and western Europe, the taxon *Sorex araneus* included a second, cryptic species: *Sorex coronatus* (e.g. Hausser et al. 1985; Neet 1989a; Hausser 1990; Hausser et al. 1990). The two species are actually defined by their karyotypes (Meylan and Hausser 1978) and have been shown to be clearcut species that do not hybridize (Neet and Hausser 1989).

Since the first records of *S. coronatus* in Germany (Olert 1973; Schwammberger 1976), some information has been published on its distribution in the Rhineland and Westphalia by Handwerk (1987). However, only very few data are available for southern Germany (Brünner and Hoffrichter 1987; Braun and Kischnick 1987; Knoch 1989).

In this paper we present new information on the distribution and ecology of *S. araneus* and *S. coronatus* in southwestern Germany (Freiburg region) and discuss their parapatric distribution in Europe, making special reference to the comparison of the distribution of the two species in southwestern Germany and western Switzerland.

Material and methods

Shrews have been trapped in the dense, herbaceous vegetation found along small rivers or in similar vegetation along woodland paths. The trapping sites lie on a transect from the Kaiserstuhl in the Upper Rhine Valley to the Feldberg in the Black Forest. 100 live traps (Sherman, Tallahassee, USA) baited with a mixture of sardines in oil and rolled oats were exposed during 23 trapping dates in 19 trapping sites. A total amount of 87 shrews was captured and determined biochemically.

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For electrophoretic determination, a blood sample of about 2 µl was taken from the tail. Blood samples were diluted in a buffer solution, analysed according to a standard technique (Hausser and Zuber 1983) and identified by the characteristic albumin patterns (Neet and Hausser 1989). As the electrophoretic technique has been tested in Switzerland only, karyological analyses were undertaken with some of the specimens of *S. araneus* and *S. coronatus* in order to ascertain the reliability of the electrophoretic method in southwestern Germany (see Neet 1989a, for a discussion of the limitations of the applicability of the technique).

Karyotypes were prepared in the laboratory from air dried mitotic chromosomes taken from bone marrow cells. The preparations were either Giemsa stained in a 4 % solution (Baker et al. 1982) or G-banded (Seabright 1971). All the *S. araneus* specimens analysed from southwestern Germany belonged to the "Vaud" karyotype with 22–24 (NF = 40) meta- and acrocentric autosomes, i.e. the same karyotype as the one used to test the biochemical determination techniques (Neet 1989a; Neet and Hausser 1989). The individuals of *S. coronatus* all had 20 metacentric autosomes (NF = 44).

Results

In the study area, *S. araneus* and *S. coronatus* appear to be parapatrically distributed, i.e. in conjunct contact, without wide zones of sympatry (Fig. 1). The corresponding list of trapping sites includes the altitudes at which the two species were caught (Table 1).

Only one species, *S. araneus*, was found in the Upper Rhine Valley near Freiburg (Mooswald) and on the Kaiserstuhl. On the lower slopes of the Black Forest (near Ehrenkirchen) and of the Zartener Becken (near Freiburg), *S. coronatus* was the only species to be captured. In the Feldberg region, *S. coronatus* was the only species found up to 730 m in the Zastler Valley, and up to 700 m in the Bruggatal and in the St. Wilhelmer Valley. The upper limit of distribution of *S. coronatus* is at about 1050 m in the Zastler Valley and 700 m in the St. Wilhelmer Valley. *S. araneus* is found between 900 m and 1450 m in the Zastler Valley and between 790 m and up to the top at the Feldberg (1496 m) in the St. Wilhelmer Valley.

As one would expect according to this altitudinal segregation pattern where *S. araneus* is found in the lowlands and higher mountain altitudes, while *S. coronatus* inhabits middle range altitudes, two contact zones were found. In these zones, as in other contact zones studied in Switzerland (Neet and Hausser 1990), the two species may coexist. The first contact zone is situated in the middle of the Zastler Valley, at 900 m, and the second one on the Schönberg, a foothill of the Black forest, at 400 m.

Discussion

Distribution of *S. araneus* and *S. coronatus* in southwestern Europe

The results presented here strongly suggest a parapatric distribution of the two species in southwestern Germany. This is consistent with the general pattern described in central and western Europe by Hausser et al. (1985). The alternating altitude distribution found here also corresponds to the one found in western Switzerland (Hausser 1978) and confirms current views on the ecology of the two species.

As a matter of fact, *S. coronatus* inhabits wide areas of northwestern Spain and most parts of France. In these countries, *S. araneus* is restricted to higher altitudes (Pyrénées, Massif central, Alpes), and the parapatric distribution is clearcut (Hausser et al. 1985).

Moving towards the east and the north of Europe, the parapatrical distribution turns out to be progressively realized on a meso-distributional level and becomes more and more difficult to visualize on a large scale. In Switzerland, *S. coronatus* is mainly present in the lowlands, the lower parts of the Jura and the Alps. In some places this species may, however, extend up to 1400 m of altitude. *S. araneus* is the dominant species above 800 m, but also occurs at low altitudes in wet habitats such as the borders of the Lake of Neuchâtel. Although a simple histogram of their altitudinal distributions suggests a wide

zone of sympatry, all detailed distributional studies have confirmed strict parapatry with contact zones never exceeding a few hundred meters (Hausser 1978; Hausser and Bourquin 1988; Neet 1989a; Neet and Hausser 1990). In Belgium, *S. coronatus* is the most common species in the western parts of the country. *S. araneus* appears in the eastern lowlands and the medium altitudes in the south of the country (Mys et al. 1985). In Holland, *S. araneus* occurs alone in the depressions in the north but the two species are believed to co-occur in the remainder of the country (Loch 1977). There is, however, some evidence that *S. araneus* is mainly distributed in areas below sea level, while *S. coronatus* occurs in areas above this level (Hausser pers. comm.). In northeastern Germany the two species co-occur over a large area: Niederrheinische Tiefebene, Mittelrhein, westfälische Bucht, Rheinisches Schiefergebirge (Hutterer and Vierhaus 1984; Handwerk 1987).

One can sum up at this point by stating that *S. coronatus* is found in areas with a balanced Atlantic climate, while *S. araneus* occurs in colder or wetter habitats, and that the parapatric distribution is decreasingly distinct as one proceeds towards the north of Europe.

Distributional ecology of *S. araneus* and *S. coronatus* in southwestern Germany

In southern Germany three climatic zones have been differentiated (Liehl and Sick 1984): 1. the warm, dry and continental Upper Rhine Valley; 2. the humid lower-altitude foothills of the Black Forest (up to 600 m), with an Atlantic climate; and 3. the heights of the Black Forest (up to 1500 m) with a typically subalpine climate and abundant rainfall. These zones closely correspond to the altitudinal distribution zones of the two species *S. araneus* and *S. coronatus*. The first species is found in the Upper Rhine Valley and above 790 m in the Black Forest, while the second is mainly found at low altitudes of the Black Forest. Interestingly, a correspondance between altitudinal zones of vegetation and the distribution of the two species has also been demonstrated in western Switzerland (Neet 1989a).

The glacier-formed St. Wilhelmer Valley is wide with high nocturnal eradiation. It opens with a gradual slope into the Bruggatal almost right angles at a very narrow point (Fig. 1). Thus, the cold air is often congested providing a rough climate. Moreover, the valley is on a lee position with rather low rainfall. In contrast, the Zastler Valley is narrow and steep sloping with several steps. It describes a slight bow and opens widely into the Bruggatal (Fig. 1). Thus, the cold air from the Feldberg heights can discharge quickly without any obstacle. As it is in a windward position, higher rainfall is noted (Schwabe-Kratochwil and Bogenrieder, pers. comm.). In the St. Wilhelmer Valley, *S. coronatus* was trapped up to an altitude of 700 m, in contrast to the climatically favoured Zastler Valley, where it can be found up to 1050 m.

An interesting parallelism with this observation has been reported for a contact zone of the *Sorex* species in a valley of the Valaisan Alps between Val d'Illiez and Champéry (Meylan 1964; Ott 1968). There, *S. coronatus* occurred on the southeastern slopes of the valley about 1 km farther uphill than on the other side of the river at the bottom of the northwestern slopes. It can be supposed that the banks along the southeastern slopes are also climatically favoured, thus enabling *S. coronatus* to reach higher into the Valley. Other similar examples have been found for the distribution of the two species in Switzerland (Hausser and Bourquin 1988).

Another distributional pattern, similar to the one found in our study area, can be expected to be found for the two *Sorex* species in northern Baden, where *S. araneus* was trapped in the Hardt Forest near Karlsruhe (Brünner unpub.) and in several locations in the south of Rastatt (Niethammer pers. comm.). *S. coronatus* was found in a beech forest at 300 m on the western slopes of the Black Forest. In this area, 26 individuals of *S.*

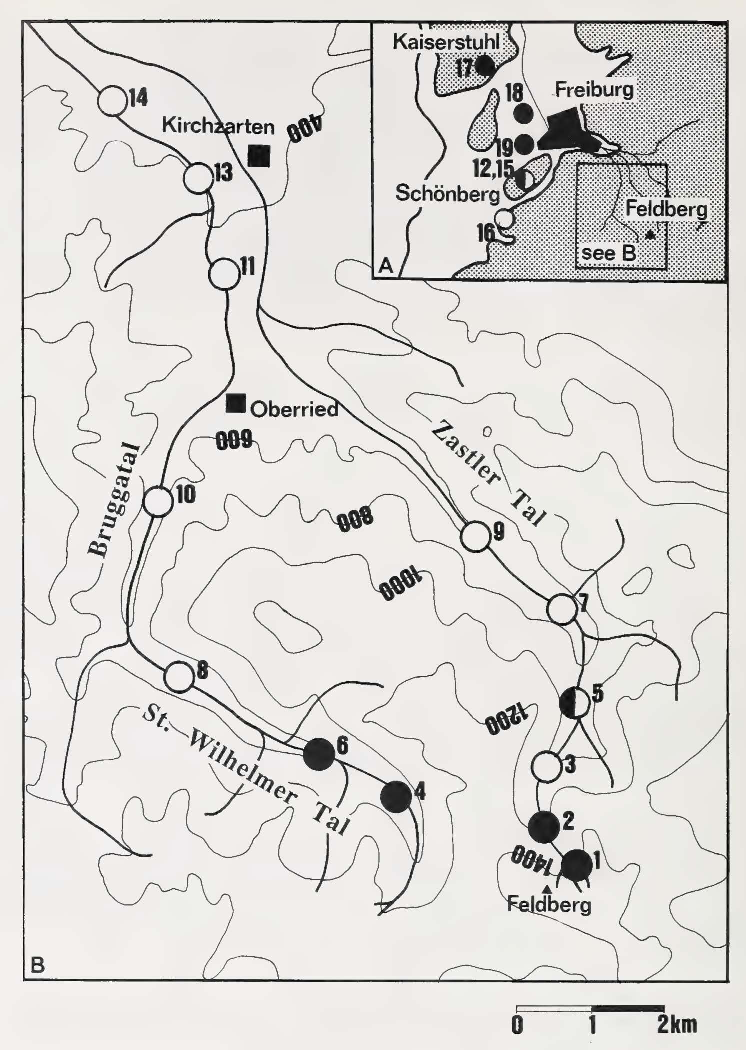


Fig. 1. Trapping sites and distribution of *S. araneus* (black circles) and *S. coronatus* (white circles) in the study area. The contact zone is given by a black and white circle. A: Freiburg region, in southwestern Germany, B: Feldberg region in the Black Forest. Locality numbers correspond to Table 1

coronatus and 3 of *S. araneus* were captured (Braun and Kischnick 1987). The shrews might have been taken from a contact zone but, at present, no additional data are available for this region.

Whereas the distribution of the *Sorex* species in the Black Forest corresponds to the situation throughout Europe described above, the occurrence of *S. araneus* in the Upper Rhine Valley, where it has already been found in Alsace by Hausser (1978), and the simultaneous absence of *S. coronatus* reveal a possible significance of drought and heat factors of the continental climate for the distributional ecology of the two species. An additional indication comes from the Catalan parts of the Pyrénées where the climate is dry, warm and Mediterranean-like and where *S. araneus* descends to low altitudes, while *S.*

coronatus is only found at 800–1500 m, although it is widespread in the Atlantic climate of northwestern Spain (Lopez-Fuster et al. 1985).

Ecological comparison of the two species

In contrast to *S. coronatus* having a relatively limited distribution in western Europe, *S. araneus* has a large distributional range from the Pyrénées to Lake Baikal in Siberia with its distributional centre in the continental east. As a species, *S. araneus* reveals greater ecological valency (Hausser and Bourquin 1988). This point is supported by some aspects of the evolutionary biogeography of the two shrew species. The British mainland, for example, with typical Atlantic climate, is only inhabited by *S. araneus* since *S. coronatus* did not arrive before its separation from the continent after the last glaciations. This species also did not succeed in passing the Alps to northern Italy. In these two regions *S. araneus* occupies all suitable habitats in the plains and in the mountain areas. As shown by Hausser and Bourquin (1988), in Switzerland *S. araneus* would be able to exist in most biotopes of the country. Its absence in the lowlands can more convincingly be explained by competition pressure going out from *S. coronatus* than by autoecological constraints (Neet and Hausser 1990). It should, however, be pointed out that *S. araneus* is not a simple species, but consists of several chromosomal types (e.g. Searle 1984; Hausser et al. 1985; Hausser et al. 1986; Reumer and Meylan 1986). To what extent are these races differentiated from an ecological point of view is not yet known and, obviously, this point may be of crucial importance in explaining the apparently wide ecological valency of *S. araneus*.

The principle stating that ecologically identical species cannot coexist (Gause 1934) is now widely accepted (Begon et al. 1986). As a consequence of the general similarity of *S. araneus* and *S. coronatus*, competition is an important factor in the lack of overlap of their distributional ranges (Hausser 1978; Neet and Hausser 1990). An ecological field analysis in Switzerland revealed that in two contact zones, the two species coexisted over a

Table 1. **List of trapping sites in southwestern Germany, classified by their altitudes**

Altitude (m a.s.l.)	Species	n (ind.) *S. araneus*/ *S. coronatus*	No.	Locality
1450	●	1/0	1	Feldberg, near top
1230	●	1/0	2	Feldberg, Zastler Hut
1050	○	0/1	3	Upper Zastler Valley
900	●	2/0	4	Upper St. Wilhelmer Valley
900	◐	3/3	5	Middle Zastler Valley
790	●	2/0	6	Upper St. Wilhelmer Valley
730	○	0/1	7	Lower Zastler Valley
700	○	0/7	8	Middle St. Wilhelmer Valley
600	○	0/1	9	Lower Zastler Valley
540	○	0/5	10	Bruggatal, near Oberried
420	○	0/2	11	Zartener Becken, near Oberried
400	◐	1/1	12	Schönberg, near Ebringen
390	○	0/1	13	Zartener Becken, near Kirchzarten
360	○	0/2	14	Zartener Becken, near Freiburg
350	○	0/1	15	Schönberg, near Ebringen
300	○	0/3	16	Border of Black Forest, near Ehrenkirchen
270	●	3/0	17	Kaiserstuhl, Lilienta l
230	●	4/0	18	Mooswald, northwest of Freiburg
215	●	42/0	19	Mooswald, southwest of Freiburg

Black circles = *S. araneus*, white circles = *S. coronatus*, black and white circle = contact zone. Locality numbers correspond to Fig. 1

limited zone of overlap by selecting different microhabitats, those of *S. araneus* having a thicker litter layer and higher soil humidity (Neet and Hausser 1990). It was also shown that *S. araneus* and *S. coronatus* occupy the same trophic niche in their zones of contact (Neet 1989a) and that equal intensities of intra- and interspecific competition for food as a limiting factor lead to interspecific territoriality (Neet 1989b). In other words, the two species do differ in terms of their ecoclimatic adaptations but are still too similar to coexist. This example thus illustrates the usefulness of the principle of limiting similarity proposed by Mac Arthur and Levins (1967).

If the high ecological similarity of *S. araneus* and *S. coronatus* does not allow sympatrical distribution, and although the contact zones we observe today seem to be relatively stabilized, one may suppose that, on an evolutionary time scale, one species will dominate the other and, with climatic changes, will replace it over an appreciable geographical space. This is how the distributional ecology of *S. araneus* and *S. coronatus* has been interpreted, since the actual distribution of the two species bears several indications that *S. coronatus* has forced *S. araneus* up to the north and east of Europe since the last glaciations. Moreover, the limited adaptations of both species to regionally or locally different climates in connection with mutual exclusion are considered to be characteristics of an early stage of ecological differentiation (Hausser 1984; Hausser et al. 1985).

The results presented here confirm the parapatric interpretation (e.g. Hausser et al. 1985; Hausser and Bourquin 1988) especially since there is a clear similarity between the situation in southwestern Germany and that in western Switzerland (Table 2). In central and northern Germany, the situation is less clear and the distribution is more mosaic-like. In that area, the distribution of the two species is sometimes considered as sympatrical (Hutterer pers. comm.). Handwerk (1987) reported ratios of *S. araneus*: *S. coronatus* of 1:1 to 1:3 for the plains of the Niederrhein and the Cologne–Bonn region, and 2:1 ratios

Table 2. **Comparison of the distributional ecology of *S. araneus* and *S. coronatus* in southwestern Germany and western Switzerland**

Data for western Switzerland are taken from Neet 1989a

	Southwestern Germany	Western Switzerland
Altitude range		
S. araneus	215–1450 m	380–1950 m
S. coronatus	300–1050 m	490–1340 m
Type of distribution	parapatric	parapatric
Relative habitat preferences		
S. araneus	cold (continental)	wet and cold
S. coronatus	warm (Atlantic) balanced humidity	dry and warm
Breadth of contact zones	200–2000 m[a]	100–1000 m[b]
Ecological relationship in the contact zones		Habitat selection in response to interspecific competition Interspecific territoriality

[a] The breadth of the contact zones was estimated as follows: in the Zastler Valley, the breadth was estimated to be equivalent to the length of the trapping area, i. e. 200 m; in the St. Wilhelmer Valley the maximal breadth was estimated to be of 2000 m, which corresponds to the distance between capture points 6 and 8 (Fig. 1). – [b] Neet (1989a) indicates breadths around 100 m. However, in patchy areas (woodlands alternating with grasslands) it is difficult to estimate a precise value (see Neet and Hausser 1990). However, maximal values around 1000 m have been estimated.

for the adjacent regions of medium altitude. NEET and HAUSSER (1990) consider that the work of HANDWERK (1987) lacks sufficient detail to ascertain whether the two species are sympatrically or parapatrically distributed in that area. A detailed ecological study might reveal local differentiation, which may be very subtle, as in the Swiss contact zones. Nevertheless, an alternative hypotheses exists and is due to the simple fact that resource availability influences interspecific competition. In the contact zones studied by NEET and HAUSSER (1990), there is evidence that food was a limiting factor (NEET 1989a) and that competitive pressure induced interspecific territoriality (NEET 1989b). If there are no limiting ressources, the situation may change. An example is given in the work by LLEWELLYN and JENKINS (1987) on the cricetids *Peromyscus maniculatus* and *P. truei*, where it was shown that there are seasonal changes in overlap of microhabitat niche, and that these changes may be explained by the degree of resource scarcity. In one of the contact zones studied in Switzerland, it was shown that the competitive pressure between *S. araneus* and *S. coronatus* is present throughout the year (NEET and HAUSSER 1990). However, the situation may be different in central and northern Germany. A seasonal variation in competitive pressures is a realistic hypothesis and may result in variations of the degree of overlap between the two species and limited sympatry.

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Zusammenfassung

Eine parapatrische Szenerie: Die Verbreitung und Ökologie von Sorex araneus und Sorex coronatus (Insectivora, Soricidae) in Südwestdeutschland

Die Verbreitung von *Sorex araneus* und *Sorex coronatus* in Südwestdeutschland wurde in einem Transekt vom Oberrheingraben zum Feldberg im Schwarzwald untersucht. Die Artbestimmung geschah mittels einer Polyacrylamid-Gelelektrophorese des Gesamtbluteiweißes. Im Untersuchungsraum waren die beiden Arten parapatrisch verbreitet, und dies in Form einer alternierenden Höhenverbreitung. *S. araneus* wurde im Oberrheintal und am oberen Feldberg angetroffen, *S. coronatus* in den unteren und mittleren Schwarzwaldlagen. Im klimatisch begünstigten Zastler Tal reicht die Verbreitung von *S. coronatus* 400 Höhenmeter weiter talaufwärts als im kälteren und rauheren St. Wilhelmer Tal. Zwei Kontaktzonen, eine obere und eine untere, wurden ausfindig gemacht. Im Untersuchungsgebiet können die beiden Arten als höhenvikariierende Arten bezeichnet werden. Die Ökologie und Verbreitungsgeschichte von *S. araneus* und *S. coronatus* wird anhand der bisher bekannt gewordenen Daten über ihre Lebensräume diskutiert. *S. araneus* besiedelt Gebiete mit eher kontinentalem Charakter sowie Lebensräume mit nassen und trockenen Böden. Dagegen bevorzugt *S. coronatus* atlantisches Klima und ausgeglichene Bodenfeuchtigkeit.

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Population dynamics of the Red squirrel in Bavaria

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Abstract

Describes the population dynamics of the red squirrel *(Sciurus vulgaris)* in Bavaria since the early 1970s. A decline in the population of squirrels was found between 1970 and 1980, while recently an increase was recorded. The decline can be attributed to reproductive waves caused by mast years of coniferous trees. The recent increase can be explained by general forest decline, since damage to trees desynchronizes seed production and squirrels are provided with a constant food resource over a number of years.

Weather conditions were found to be unimportant for the population dynamics of squirrels. For the beech marten *(Martes foina)*, however, a negative correlation could be demonstrated between number of squirrels and this predator at one study site.

Introduction

Compared to birds the available data on long-term fluctuations of medium-sized mammals are very rare. This is due to the difficulties to trap and count these animals within a reasonable period of time. Even for diurnal species like the red squirrel *(Sciurus vulgaris)* only a limited amount of information is available. Long-term series are badly needed to document the full range of patterns in the population dynamics of mammals. In game biology there is a long tradition to use hunting bags or other indirect measures to document fluctuations in game animals (for a recent example see Potts et al. 1984). We followed this line of investigations and present indirect density indices to describe the dynamics of the red squirrel in Bavaria. We concentrate on the following questions:

1. Are there any long-term trends in the population of squirrels in Bavaria? In two reports we suggested that there was a decline in numbers of squirrels since the early 1970s (Brandl 1983; Reichholf 1983).
2. Is the dynamics of the squirrel populations similar in different regions of Bavaria?
3. The main food of the red squirrel is the seeds of coniferous trees (Wiltafsky 1978). Many studies have shown that the populations of squirrels follow seed production (Formosov 1933; Pulliainen 1984; Reichholf 1974). Is this pattern also evident within our sets of data?
4. The red squirrel is the prey of several predators such as the pine and beech marten (*Martes martes, M. foina;* Stubbe 1988). Do these species have some influence on the populations of the red squirrel?

Material and methods

In the following we name each data set by its geographical location (see Fig. 1):

1. Pressath: This data set consists of specimens delivered to a taxidermist between September and March from 1965/66 onwards to 1982/83 with a gap between 1967/68 and 1972/73 (550 individuals; Brandl 1983). The working period of the taxidermist was not constant over the years. We used the

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Fig. 1. Geographical location of the investigated areas in Bavaria

number of mammals and birds to standardize red squirrel data and calculated percentages of red squirrels delivered to the taxidermist.

Around Pressath the dominating types of vegetation are spruce forests *(Picea abies)* and at poorer sites pine forests *(Pinus sylvestris)*. Altitudes range from about 400 to 600 m NN.

2. Bad Berneck: Similar to Pressath these data are specimens delivered to a taxidermist between 1970 and 1988 (922 individuals). This taxidermist worked over the entire year. We standardized the data because the overall working effort appeared to vary from year to year. The number of delivered birds was used as an independent measure of the working effort. Numbers of red squirrels are expressed in individuals delivered per 100 birds.

   Bad Berneck is situated within the Fichtelgebirge. Spruce forests are the dominating type of vegetation, and the altitudes range from 500 to 1000 m. At higher altitudes winters may be quite severe.

   For this area we have also data about weather, seed production of the spruce and dynamics of one potential predator.

   a. Monthly information of rainfall and temperature was available for Bayreuth, only 10 km from Bad Berneck.
   b. The forest authorities estimate the seed production in four categories: "Vollmast" = very high

seed production, "Halbmast" = good seed production, "Sprengmast" = low seed production and no seed production. We ranked each year on this scale from 0 to 3 and allowed for intermediate values according to information of the forest authorities (available years 1971 to 1988).

c. The number of martens delivered to the taxidermist (pine and beech marten) may be used as an indicator of the predator density. The pine marten is rather uncommon in the area around Bad Berneck, so we concentrate on the beech marten. Data were standardized similar to those for squirrel numbers.

3. Inn: These data are from squirrel sightings made during standard excursions between 1971 and 1982 (153 records; Reichholf 1983).
4. B 12: Road kills are often good indicators of the population dynamics of medium-sized mammals. The B 12 data sets are the sums of road kills during a year along the federal highway B 12 between Munich and Bad Füssing (89 individuals; Reichholf 1983; 1976–1988). The killed martens were also counted along the same route.
5. Garmisch-Partenkirchen: Data are from squirrel sightings along three transects (1979 to 1988; 195 records), situated at the lower mountain forests about 800 to 900 m NN and were sampled twice each month. The dominating tree species is the spruce, but deciduous species of trees are also present. Winters may be severe with snow cover between November to April.

Results

Phenology

The seasonal distribution of data (Inn, B 12, Garmisch-Partenkirchen) is plotted in Fig. 2. The phenological patterns are similar for Inn and Garmisch-Partenkirchen ($r = 0.55$; $P < 0.05$; one-tailed). No road kills were found during January and December in contrast to the data based on squirrel sightings. All three plots showed a minimum during July.

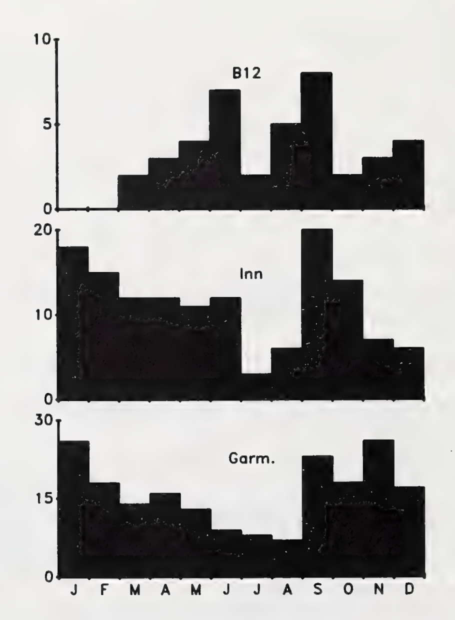


Fig. 2. Seasonal distribution of road kills (B 12) and sighting records (Inn, Garm. = Garmisch-Partenkirchen) of the red squirrel, given as the sum of sightings or road kills recorded within each month

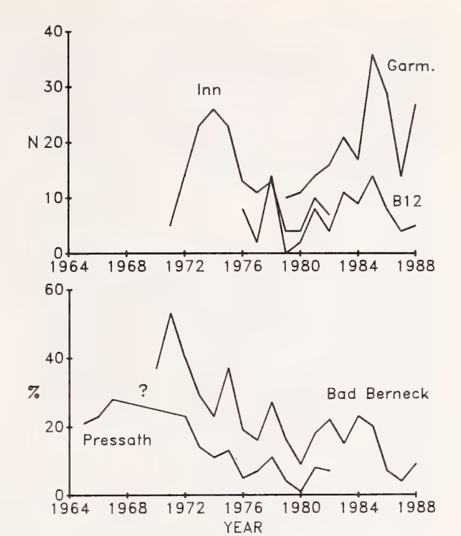


Fig. 3. Population fluctuations of the red squirrel in different areas of Bavaria. For the areas Inn, B 12 and Garmisch-Partenkirchen (Garm.) the sum of all sightings or road kills within each year is given. The data from Bad Berneck and Pressath are relative indices calculated as percentages of squirrels delivered per all animals (Pressath) or squirrels delivered per 100 birds (Bad Berneck; see Material and methods)

Population dynamics

In Fig. 3 all data sets are plotted across the years studied. The data from northern Bavaria (Bad Berneck and Pressath) show a clear decline in the squirrel populations. This decline is also apparent within the Inn data, but with an obvious peak in 1974. Since 1980 there seems to be a slight increase of squirrel populations, evident in all data sets covering this period. Furthermore, the plots show a rough concordance in minor peaks (e.g. 1975, 1978, 1983, 1985). Table 1 presents the correlation coefficients between sampling areas: all correlation coefficients are positive and six from ten are significant.

Table 1. **Matrix of pairwise correlation coefficients (upper half of the matrix) between the squirrel density indices of Fig. 3**

Each coefficient measures the similarity in the population dynamics of squirrels between a particular pair of geographical locations, considering only the years with data for both areas. The lower half of the matrix gives the significance levels of the correlation coefficients (one-tailed)

	1	2	3	4	5
1 Inn	—	0.770	0.727	0.201	0.580
2 B 12	0.021	—	0.732	0.483	0.738
3 Garmisch-P.	0.137	0.008	—	0.005	0.766
4 Bad Berneck	0.265	0.047	0.495	—	0.923
5 Pressath	0.030	0.029	0.117	0.000	—

Squirrels and predators

We concentrated on the data from Bad Berneck, because this is the longest time series. In Fig. 4A we removed the negative trend apparent in Fig. 3 by linear regression. Runs with several transformations produced identical results. Firstly, some very prominent peaks are evident by the residuals, and secondly, there is a depression in squirrel densities between 1976 and 1980. This depression within the squirrel data seems to correlate with a maximum in the population index of the beech marten (Fig. 4B). A stepwise multiple regression was

performed with the squirrel data as dependent variable and years and predator density index as independent variables. The sequence of variables entering the regression was 1. year and 2. predator with a significant negative regression coefficient (see also Table 2). Fig. 5A plots the residuals from a simple regression of squirrels to years (data in Fig. 4A) against the marten index (Fig. 4B): the negative correlation between squirrels and the beech marten is evident.

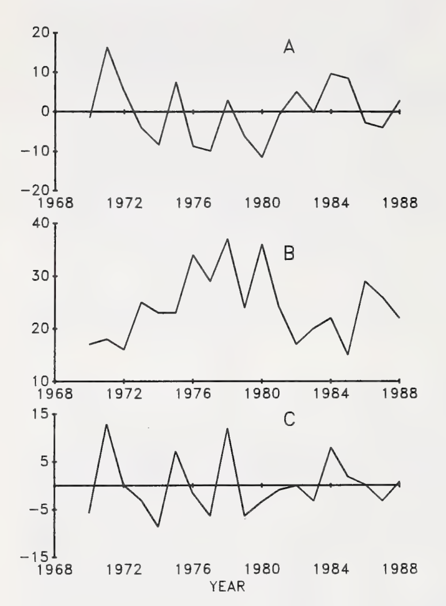


Fig. 4. A: Residuals of the red squirrel density after removing the negative trend over the years investigated. B: Dynamics of the beech marten in the same area, given as number of martens delivered per 100 birds (see Material and methods). C: Residuals of the red squirrel density after removing the trend over the years examined and the influence of the marten (all data from Bad Berneck, Fichtelgebirge)

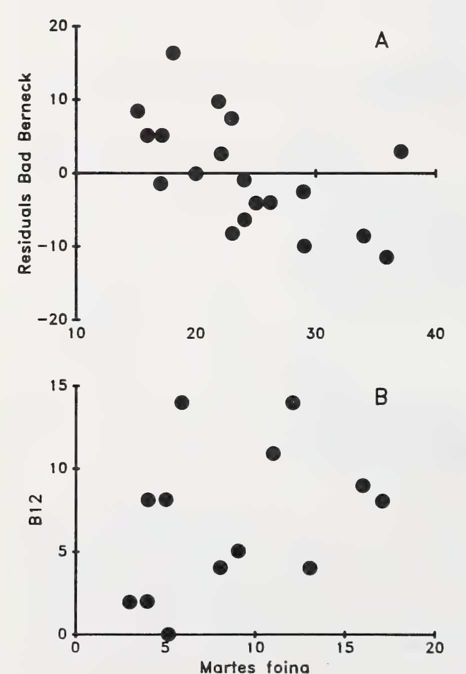


Fig. 5. A: Scatter plot of the red squirrel (after removing the negative trend over the years examined) and the populations of the beech marten (see Fig. 4 A, B; area: Bad Berneck). B: Scatter plot of road kills of squirrels and beech marten along the highway B 12

Table 2. **Stepwise multiple regression with red squirrel index from Bad Berneck as dependent variable and year, marten population and mast index of the spruce in the previous year as independent variables**

A: sequence of variables entering the regression

Step	Variable	R^2	P
1	year	0.56	< 0.001
2	marten	0.72	< 0.001
3	mast index	0.78	< 0.001

B: regression equation after step 3

Variable	Slope	Stand.slope	P
Year	−1.532	−0.78	< 0.001
Marten	−0.533	−0.35	0.02
Mast index	3.21	0.25	0.08[1]
Constant	3065		

[1] note that P is two-tailed in Table 2; in the text we used a one-tailed probability.

In Fig. 5B a scattergram was also plotted for the road kills of red squirrel and beech marten along the B 12. Contrary to the area around Bad Berneck we found no negative correlation between predator and prey (r = 0.37; P > 0.2; two-tailed).

Squirrels, food and weather

For the data set from Bad Berneck information on seed yield of spruce was available (Fig. 6B). The residuals from the multiple regression after step two in Table 2 are also shown. Seed index and residuals are significantly correlated with a time lag of one year (r = 0.48; p = 0.04; one-tailed; note that degrees of freedom have to account for the number of variables used to calculate the residuals). Table 2 shows the stepwise multiple regression of squirrel population index and the independent variables 1) year, 2) marten population and 3) mast index (one year time lag). The mast index entered the regression during the last step.

The influence of monthly rainfall and temperature patterns on the residual (Fig. 4C) for time lags for up to two years were also tested. From 60 calculated correlation coefficients

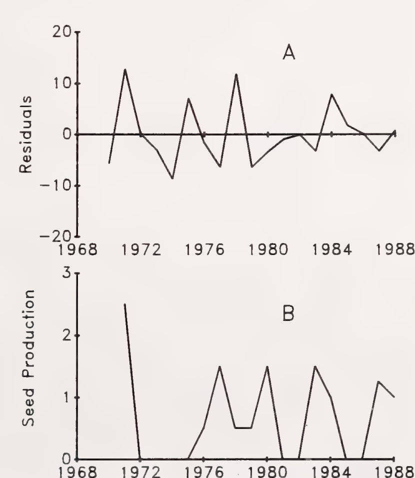


Fig. 6. A: Dynamics of the red squirrel after removing the influence of years and beech marten. B: Fluctuations in seed production of the spruce (area Bad Berneck, Fichtelgebirge)

only two were significant at the 5 % level, a result expected by chance alone. Therefore, it seems rather safe to conclude that weather conditions are unimportant for the dynamics of red squirrels.

Discussion

The seasonal distribution of the observational data and the road kills of red squirrels are quite different. During winter the red squirrel shows a reduced overall activity (Zwahlen 1975; Tonkin 1983). The reduced number of road kills are in accord with this fact. But why are so many sightings recorded during winter? The squirrel is a diurnal species with a long bimodal activity during summer, and a short unimodal pattern in winter (Tonkin 1983). In winter the peak activity is during late morning. This activity pattern may correlate with the activity of observers. Squirrels search for food during winter in the vicinity of the dreys without making longer excursions to save energy (Pulliainen 1973). That is why during transect counts squirrels are easily detected by an observer. A reduced foraging range may decrease the probability of beeing killed on the road.

Fig. 3 suggests a decline in the squirrel population in nearly all regions of Bavaria. Is this decline a natural phenomenon within the population dynamics of the squirrel, or is this decline the result of the environmental damage caused by man?

From studies in boreal regions it is well known that squirrels increase their numbers after years of a high seed yield (Formosov 1933; Pulliainen 1984). At first glance, the correlation between seed production and squirrel numbers seems to be weak in Bavaria (Table 2), but we believe that this impression is incorrect. For example Möckel (1987) described a clear increase in the red squirrel after a mast year in the West-Erzgebirge and a decline to the original density within 5 years. The availability of food after a mast year seems to improve the condition of females and thereby the probability of reproduction (Wauters and Dhondt 1989; Gurnell 1983) also under normal ambient conditions in Central Europe. The increased probability of reproduction, an increased litter size as well as better survival of young produces a population explosion in squirrels. The maximum age of red squirrels is more than 10 years, and about 1 % of individuals may reach 5 years of age or older (Wiltafsky 1978). Therefore, the explosion needs around 5 years to fade, as long as adult survival is nearly independent of seed production by trees.

1971 was one of the most important mast years of spruce within the examined time span (Reichholf 1974). As most of our data sets start in 1971 or later we are unable to document the increase in squirrel numbers: our data only show the fading of the "population wave". Furthermore, the minor mast years also produced smaller waves, and they all superposed. This scenario provides an explanation of the decline in the red squirrel since the early 1970s (Fig. 3). The negative regression coefficient of the variable year in Table 2 describes in part the lasting effects of a very prominent "population wave". The weak effect of our mast index in Table 2 is an artefact, because some of the mast-induced variation in squirrel numbers is covered by the variable year. We attribute the observed decline of the red squirrel to natural variations of the seed production of coniferous trees. The good correlations between data sets (Table 1) may be a consequence of synchronized masts across Bavaria.

Schröder et al. (1982) describe a simulation model for the capercaillie *(Tetrao urogallus)* similar to our explanation of the squirrel dynamics. Random variations in reproduction may impose long-term cycles in a species, only because adults are long-lived and independent from the factors influencing reproduction. Bad weather conditions are the cause in the capercaillie, seed production in the red squirrel. We would like to stress that the data in Fig. 3 and the simulations of Schröder et al. (1982) should act as examples for investigators studying the dynamics of long-lived species. A time series of 20 years may be

too short for a complete analysis, because historical events outside the analysed time span may have lasting and confusing effects.

The high level of the squirrel index at Pressath between 1965 and 1967 is inconsistent with the view that the dynamics of the squirrel is mainly influenced by seed production. Möckel's (1987) data indicate a very low density during that period. Consequently, one may suggest that the population density of the red squirrel dropped below the level of the late 1960s after an intermediate increase induced by spruce mast in 1971. Note that we have no data for the period around 1971 for Pressath (question mark in Fig. 3).

Perhaps some people would invoke forest decline as a factor, which may negatively influence forst animals. Damage of forests is frequent in northern Bavaria (Schulze 1989). Forest decline has been prominent since the late 1970s, but the squirrel populations have increased since 1980 (see Fig. 3; Garmisch-Partenkirchen and B 12). Furthermore, forest decline may have a positive effect on species depending on seeds. The synchronized production of seeds is reduced by the damage to trees. Every year some trees produce seeds and the food supply may be more constant compared to periods with synchronized, but unpredictable seed production. Around Garmisch-Partenkirchen nests of the crossbill *(Loxia curvirostra)* were found nearly each year in the late 1980s, whereas in the 1970s broods were only observed during mast years (Bezzel unpubl.).

In the Fichtelgebirge the beech marten is negatively correlated to squirrel density (Fig. 5A). This suggests that within certain circumstances predators have some influence on prey species (note that the B 12 data did not show such a correlation!). Squirrels are only an alternative prey of the beech marten and the densitiy of the marten is regulated by different factors: the population dynamics of the squirrel has no effect on marten populations. Pulliainen (1984) found no increase in the pine marten after an increase in squirrels. In turn, an increase in predator populations may increase predation pressure on alternative prey species. This situation is similar to the "alternative prey hypothesis" of Angelstam et al. (1984), which explains why certain animal species show synchronized fluctuations in Fennoscandia. Voles are known to fluctuate with a cycle of about 3 to 4 years and the dynamics of the predators (like the red fox *Vulpes vulpes*) are coupled to this prey. When the main prey declines the predators turn to alternative prey species inducing a cylce on these prey species. Our explanation implies no fluctuations in the main prey of the beech marten; we only hypothesize that an increased predator density should have an inhibiting impact on the alternative prey. This is similar to Janzen's (1976) explanation of the low reptile biomass in Africa. Janzen believes that many predators are able to maintain high population sizes because of the large herbivore biomass. The carnivores impose predation pressure on minor prey species and lower the reptile biomass (Janzen 1976; but see Kreulen 1979).

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Zusammenfassung

Populationsdynamik des Eichhörnchens in Bayern

Für fünf Gebiete Bayerns werden die Populationsschwankungen des Eichhörnchens *(Sciurus vulgaris)* dargestellt. Zwischen 1970 und 1980 war eine Abnahme der Eichhörnchen zu beobachten, seit 1980 hingegen kam es wieder zu einer leichten Zunahme. Die Abnahme ist wohl keine Folge menschlicher Eingriffe, sondern kann auf Reproduktionswellen zurückgeführt werden, die durch die Mastjahre der Fichte bedingt sind. Die Zunahme seit 1980 wird als Folge des Waldsterbens diskutiert, da die Schädigung der Nadelbäume zu einer Desynchronisation der Zapfenproduktion geführt hat. Damit stand den Eichhörnchen eine konstante Nahrungsquelle zur Verfügung.

Wetterfaktoren scheinen die Dynamik der Eichhörnchenpopulation nicht zu beeinflussen. Dagegen finden wir eine negative Korrelation zwischen Steinmarder *(Martes foina)* und Eichhörnchen.

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An experiment to test the consumption of arboreal food by Wood mouse *Apodemus sylvaticus*

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Abstract

Analysed factors affecting the arboreal feeding activity of wintering wood mice in a set of woodlots in central Spain. Stations were baited with acorns on branches, trunk and ground of 429 trees to test the arboreal behaviour of mice. Acorn intake on branches was positively and significantly related to accessibility of food but not to mice abundance. The best predictor of food consumption on branches was, however, the ground-trunk acorn intake, suggesting that this variable was a good index of the scarceness of food. We conclude that morphological constraints in the arboreal ability of the species were evident.

Introduction

Wood mice *(Apodemus sylvaticus)* are recognized as expert climbers (Holisova 1969; Le Louarn and Saint-Girons 1977; Gurnell 1985), but there is a lack of information about the factors determining this behaviour (Montgomery and Gurnell 1985). The use of arboreal substrata may be subject to conflicting factors, such as predation risks, resource availability, and others (e.g. King 1985; Brown 1989; Simonetti 1989). The trade-off between risks and benefits in a particular microhabitat may change, however, as a result of increased pressures on other microhabitats nearby. For example, high population densities may force some individuals to use less preferred resources (Fretwell 1972; Gurnell 1985). Thus, decreased availability of food, frequently related to peak densities (Flowerdew 1985; Hansson 1985), may stimulate the exploratory behaviour of rodents (Stickle 1979; Montgomery and Gurnell 1985; Pennycuik and Reisner 1989). Morphological constraints and travel expenditures seem to be the another relevant factor influencing the selection of feeding microhabitats (Wiens 1973; Gurnell 1985; Brown 1989; Simonetti 1989).

In this work, we explore the incidence of mice abundance and food accessibility on the arboreal feeding activity of wintering wood mice *(Apodemus sylvaticus)* in Holm oak woodlots of central Spain. The winter is a period with heavy food constraints for many temperate endotherms (Newton 1981; Merrit 1984), so mice arboreality could be stimulated in this season.

Study area

The study area is located in Burgos province, central Spain. Average altitude is 850 m and phytoclimatic conditions are inland mediterranean, with long and cold winters (Rivas-Martínez 1981). The area has a deforested agricultural landscape, with extensive cereal cropping and sheep grazing as main usages. Some tracts of the original forests remain, with a dominant vegetation formed by Holm oaks *(Quercus rotundifolia)* and shrubs of the genera *Cistus, Genista, Thymus* and *Lavandula*. These woodlots support wintering populations of wood mouse, but mice are scarce during winter in the surrounding fields (Tellería et al. 1990; see also Alcántara 1986). Previous trapping work showed that rodent species other than wood mice are scarce or absent in these forests; Common voles *(Microtus arvalis)* settle some grassy sectors and Garden dormice *(Eliomys quercinus)* hibernate throughout the winter. Seventeen isolated woodlots, ranging from 0,1 to 280 ha (Table), were studied in order to evaluate the use of arboreal preys by mice.

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The 1988 autumn crop of acorn, preceding the study winter, was very scarce; at the start of December only 0.8 % (n = 131) of the Holm oaks beared fruits and 3.2 % (n = 158) had shed acorns to the surrounding ground. By the 20th of January a high degree of depletion was evident, since tree and ground acorns were lacking in most woodlots.

Material and methods

Food accessibility

Holm oak half-acorns were pierced with wire and tied round branches with different diameters and at different distances from the tree basis to test the relationship between the arboreal feeding efficiency of mice and food accessibility. The wood mouse is an omnivore, and includes fruits in its diet (Obrtel and Holisova 1983; Hansson 1985), so that we could assume that Holm oak acorns should be profitable baits. Acorns were arranged during one dark night in each woodlot, and placed and controlled in the same order, so all acorns were exposed the same time. Two experiments were carried out in 1989, from 12 to 16 January and from 2 to 5 February. One half-acorn per tree were tied on 429 trees distributed among the 17 Holm oak forests. Numbers of acorns ranged from 6 to 49 in each experiment (Table), according to a logarithmic function of forest area. Branch diameter was estimated visually for 380 acorns; distance from ground was estimated for each acorn as the shortest path from the base of the tree. Branches ranged from 0.3 to 10 cm in diameter, with the majority between 0.5 and 3 cm (87.9 %). Distances ranged from 0.5 to 12 m, those between 2 and 4 m accounting for 78.5 %. Half-acorns were also placed on the trunk, 1.5 m above ground and on the base of the trunk, in the same trees, to assess the global food searching incidence by mice in each forest.

As wintering mice mainly use underground burrows (Dufour 1978; Montgomery and Gurnell 1985), accessibility of arboreal food should be negatively related to ground distance, and positively to branch diameter for morphological reasons. Since separate analysis of these two variables can produce confounding results, a difficulty index (ID) was estimated for each acorn as the product of distance by the inverse of diameter; ID ranged from 0.2 to 26.7, with values between 0.2 and 6 summing 92.1 %. We calculated mean values of distance, diameter and ID for each forest. Percentages of acorns preyed upon by mice were used as estimates of feeding incidence in the three positions sampled. Acorn use on ground was significantly associated with acorn use on trunks ($r = 0.824$, $p < 0.001$, 15 d.f.), therefore both positions were analysed together. Acorn intakes in January and February were positively correlated ($r = 0,78$, $p < 0.001$, 15 d.f.; see Tellería et al. 1990), so both samples were pooled. Preyed acorns were easily recognizable by teeth marks and fecal rests. The acorns preyed by birds or lost were not considered in the analyses.

Mice abundance

At the beginning of March 1989, 213 stations were provided with two snap-traps during two consecutive nights (Smith et al. 1975); number of traps ranged from 12 to 196, according to woodlot area. Abundance indexes were obtained as the number of individuals captured by trap in each forest (Table; see Tellería et al. 1990, for more details on the trapping design). Wood mouse was the only species caught.

Statistical analyses were made according to Sokal and Rohlf (1981) and Zar (1984). Mice abundance and acorn intake rates were arcsin transformed, and distance, diameter and ID values logtransformed.

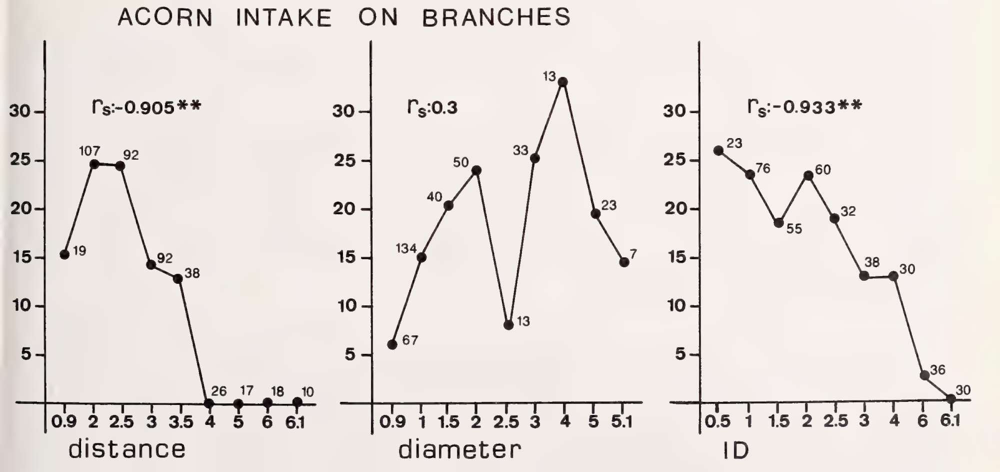
Results

Branch acorns were exclusively preyed upon in locations placed between 0.5 and 3.5 m from the base of the tree; 71 acorns arranged between 3.6 and 12 m remained untouched, most of these placed in the canopy edge. Acorns were consumed from branches of all diameters, although twigs of less than 1 cm supported the lowest predation (see Figure). Relationship between acorn predation rate and accessibility was first explored classifying the acorns in 9 classes according to distance, diameter and ID. The results show that the proportion of preyed acorns decreased significantly with the increase of distance and ID, but a diameter response was not obvious (Figure). ID was the only variable among these three used in the following analyses, since it may be considered a synthetic index representative of acorn accessibility.

Table. **Area, mice abundance (No. individuals/trap × 100), number of acorns placed and controlled (N) and acorn intake rates (percentage of acorns preyed) in each forest**

woodlot area (ha)	mice abundance	acorn intake ground N	ground %	trunk N	trunk %	branches N	branches %
0.1	17.0	12	(100.0)	12	(83.3)	12	(33.3)
0.3	75.0	12	(91.7)	12	(75.0)	12	(0.0)
0.3	50.0	12	(100.0)	12	(83.3)	12	(41.7)
0.3	50.0	11	(81.8)	10	(80.0)	12	(33.3)
0.3	40.0	12	(83.3)	12	(50.0)	12	(25.0)
0.3	12.5	11	(36.4)	10	(50.0)	12	(0.0)
0.6	33.3	11	(72.7)	11	(72.7)	12	(41.7)
0.7	29.2	12	(75.0)	12	(41.7)	11	(9.1)
0.7	20.8	12	(91.7)	10	(90.0)	10	(45.5)
0.8	33.3	12	(100.0)	12	(100.0)	12	(83.3)
1.2	37.5	12	(66.7)	12	(75.0)	12	(33.3)
1.3	45.8	12	(50.0)	12	(50.0)	12	(16.7)
2.0	29.2	10	(90.0)	10	(80.0)	9	(37.5)
12.0	21.6	49	(44.9)	49	(40.8)	48	(2.1)
16.0	25.0	49	(65.3)	49	(59.2)	49	(32.7)
150.0	2.6	85	(47.1)	85	(12.9)	86	(5.8)
280.0	4.6	89	(38.2)	89	(18.0)	85	(3.5)

According to relationships between the feeding incidence on branches and the independent variables estimated in each forest, ID accounted for more variation ($r = -0.569$, $p < 0.05$; $R^2 = 32.4$ %) than mice abundance ($r = 0.183$, n.s.; $R^2 = 3.3$ %), but this was less than that accountable for acorn intake on ground and trunks ($r = 0.711$, $p < 0.01$; $R^2 = 50.6$ %). These results were supported by partial correlation analyses of feeding incidence on branches with 1) mice abundance and ID: partial r values were 0.287 (n.s.) for abundance and −0.599 ($p < 0.02$) for ID; 2) with mice abundance and ground-trunk acorn intake: $r = -0.299$ (n.s.) and $r = 0.731$ ($p < 0.01$), respectively; and 3) with ground-trunk acorn intake and ID: $r = 0.649$ ($p < 0.01$) and $r = -0.457$ (n.s.), respectively.



Relationships of acorn intake on branches (in percentages) to distance (m), diameter (cm) and acorn accessibility (ID). r_s is the Spearman's rank correlation coefficient; **: $p < 0.01$

Discussion

Mice consumed acorns placed in branches regardless of diameter and up to a distance 3.5 m from the tree base, but not further away. Thus, our results agreed with the arboreality of the species, although a limit in its arboreal exploration was apparent in our study. This could be directly due to constraints in movement ability of mice in trees, but other factors may operate simultaneously (CARACO 1980).

In crowded conditions, some island populations of rodents increase their resource partitioning, with younger individuals obliged to live in suboptimal patches (GLIWICZ 1984; see also LOMNICKI 1988). Therefore, we should expect a rise of food demands with the increase in mice density in the woodlots studied, and hence a searching increase towards the least accessible acorns. Since this expected relationship did not occur, it is plausible that even the higher densities obtained were very low and mice did not need to explore the most inaccessible acorns; actually, mice abundance accounted for a relatively low variance of the acorns consumed on ground and trunks ($R^2 = 26.2$ %). On the other hand, if resource levels differed among woodlots, the total acorn intake would be a better estimator of trophic stress than mice abundance. In fact, some small woodlots with "low" abundances of mice gave the highest intakes (Table). This view is consistent with our results, suggesting that under conditions of limited food supply mice could search for supplementary food above ground. Also, an increase of searching activity in the adjacent fields, including dispersal behaviour, could be an alternative response. Exploratory and dispersal ability, agricultural field use and habitat tolerance in the Wood mouse (JONGE and DIENSKE 1979; JENSEN 1982; GEUSE et al. 1985; GURNELL 1985; WOLTON and FLOWERDEW 1985), suggest that this response would be more profitable than an exploratory increment towards presumably little accessible substrata, such as branches, but at present experimental evidence is lacking.

In conclusion, the findings of our experiment, namely, the clear limit observed in the ability of the Wood mouse to obtain arboreal food, and the association of acorn use on branches with ID, suggest morphological constraints of this species in the searching of tree food, and would indicate a negative yield in the handling of distant arboreal preys. At the same time, this study suggests that mice are capable of overcoming local situations of food scarcity on the ground by using alternative arboreal resources.

In another context, the decreasing gradient observed in the feeding incidence of mice from ground to trunk-branches, implies potential consequences for forest avian species feeding mainly on the ground and trunks (e.g. pariforms; see ULFSTRAND 1977). The high densities of mice registered in island conditions in this and other works (e.g. GLIWICZ 1984; GEUSE et al. 1985), point out a probable competition between birds and rodents whose main biological effects are unknown at present, although composition and densities of avian species could be affected. As JANZEN (1986) recently expressed, other topics than customary (area, distance to continent, habitat diversity, etc.) are involved in island biology; the ones related to high densities of generalist animals, such as wood mice (FLOWERDEW 1977; LE LOUARAN and SAINT-GIRONS 1977), represent an important threat for stenoecious or scarce organisms.

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Zusammenfassung

Ein Experiment zur Ermittlung der Nahrungsaufnahme der Waldmaus (Apodemus sylvaticus) auf Bäumen

Untersucht wurden mehrere Faktoren, die die Aktivitäten von Waldmäusen bei der Nahrungssuche auf Bäumen beeinflussen. Dazu wurden in mehreren Waldparzellen in Zentralspanien während des Winters Eicheln am Boden, an Stämmen und auf Zweigen von 429 Bäumen angeboten. Der Konsum von Eicheln auf Zweigen war positiv und signifikant korreliert mit der Erreichbarkeit der Nahrung, aber nicht mit der Häufigkeit der Waldmäuse. Die Eicheln wurden vornehmlich von Boden und Stämmen aufgenommen, aber auch von Zweigen unterschiedlicher Stärke, allerdings nur bis zu 3,5 m Höhe. Dieses weist auf Grenzen der Art hin, den arboricolen Lebensraum zu nutzen.

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Genetic differentiation in four species of *Apodemus* from Southern Europe: *A. sylvaticus, A. flavicollis, A. agrarius* and *A. mystacinus* (Muridae, Rodentia)

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Abstract

Genic variability was estimated for four *Apodemus* species from Southern Europe by electrophoresis at 20 loci. Genic divergence data agree well with the subgeneric classification, *A. agrarius* (subgenus *Apodemus*) being very distant from the three other species (subgenus *Sylvaemus*), as was previously shown by Gemmeke (1980) using 11 loci. However, the large divergence between these two groups suggests that their taxonomic relationships should be revised. The morphological overlap between *A. sylvaticus* and *A. flavicollis* is confirmed throughout Southern Europe which stresses the use of biochemical methods for unambiguous identification of specimens. The karyological analysis of samples of *A. sylvaticus, A. flavicollis* and *A. agrarius* revealed chromosomal variation in only one individual (*A. flavicollis* with 2 n = 49 in Bulgaria).

Introduction

The genus *Apodemus* is one of the most widespread noncommensal rodent groups in the Paleartic. In the Western part of their range, the use of biochemical genetics has proven extremely useful in unambiguously discriminating morphologically similar species. This has been the case for *A. sylvaticus* and *A. flavicollis*, in particular, which although easily distinguishable in Central and Northern Europe, show a morphological overlap in the more southern areas. That this overlap is due to clinal variation in size and pelage color following opposite trends in both species and not to hybridization, has been shown by a number of authors (Niethammer and Krapp 1978; Gemmeke 1980; Benmehdi et al. 1980; Nascetti and Filippucci 1984). This discrete morphological variation seems to be a general trait within the subgenus *Sylvaemus* (*A. mystacinus* excepted), although genic differentiation as measured by electrophoretic methods is quite extensive. Recent studies of more eastern populations suggest that this subgenus will most likely reveal a complex of species (Niethammer 1969; Darviche et al. 1979; Gemmeke and Niethammer 1982).

Karyotypic variability is also well documented within the subgenera *Sylvaemus* and *Apodemus*. All species carry 48 chromosomes but differ in the NF number showing that chromosomal evolution has proceeded mainly by pericentric inversions (Kral 1970; Soldatovic et al. 1975; for a review see Zima and Kral 1984).

The evolutionary relationship between *Apodemus* species was previously investigated at 11 loci by Gemmeke (1980). The genetic differentiation between *Apodemus* species belonging to the two subgenera *Sylvaemus (A. sylvaticus, A. flavicollis, A. mystacinus)* and *Apodemus (A. agrarius)* is here extended to populations from Greece, Bulgaria and Spain for which morphological, chromosomal and allozymic data at 20 loci are presented.

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Material and methods

Specimens belonging to four species of the genus *Apodemus* (*A. sylvaticus, A. flavicollis, A. mystacinus* and *A. agrarius*) were live-trapped in localities (see Figure 1 for names) from five southern European countries. Nine populations were analyzed for genic variability: France (1), Italy (2), Greece (3, 4, 5, 6), Spain (7) and Bulgaria (8). Starch gel electrophoresis techniques are described in Pasteur et al. (1987). A total of 20 loci were analysed: alcohol dehydrogenase *(Adh)*, alpha-glycerophosphate dehydrogenase *(alpha-Gpd)*, albumin *(Alb)*, amylase *(Amy-1)*, glutamate oxaloacetate transaminase *(Got-1)*, glucose phosphate isomerase *(Gpi)*, hemoglobin *(Hbb)*, isocitrate dehydrogenase (*Idh-1* and *Idh-2*), lactate dehydrogenase (*Ldh-1* and *Ldh-2*, respectively coding for the A and B subunits; see Engel et al. 1973), the regulator gene for *Ldh-2* in red cells *(Ldr)*, NAD-dependent malate dehydrogenase (*Mdh-1* and *Mdh-2*), NADP-dependent malate dehydrogenase *(Mod-1)*, nucleoside phosphorylase *(Np)*, phosphoglucose dehydrogenase *(Pgd)*, phosphoglucomutase *(Pgm)*, sorbitol dehydrogenase *(Sdh)* and superoxide dismutase *(Sod)*. Allelic designations were determined by comparison to the mobility of the most frequent allele in *A. sylvaticus* which was arbitrarily assigned the value 100. The HBB pattern in *Apodemus* consists in two spots, the slower one showing no variation, so the genetic variability scored refers only to variation in mobility of the faster migrating spot. Genetic variability measures, genetic distances (Nei 1978) and the UPGMA phenogram were computed and performed using the BIOSYS-1 program of Swofford and Selander (1981).

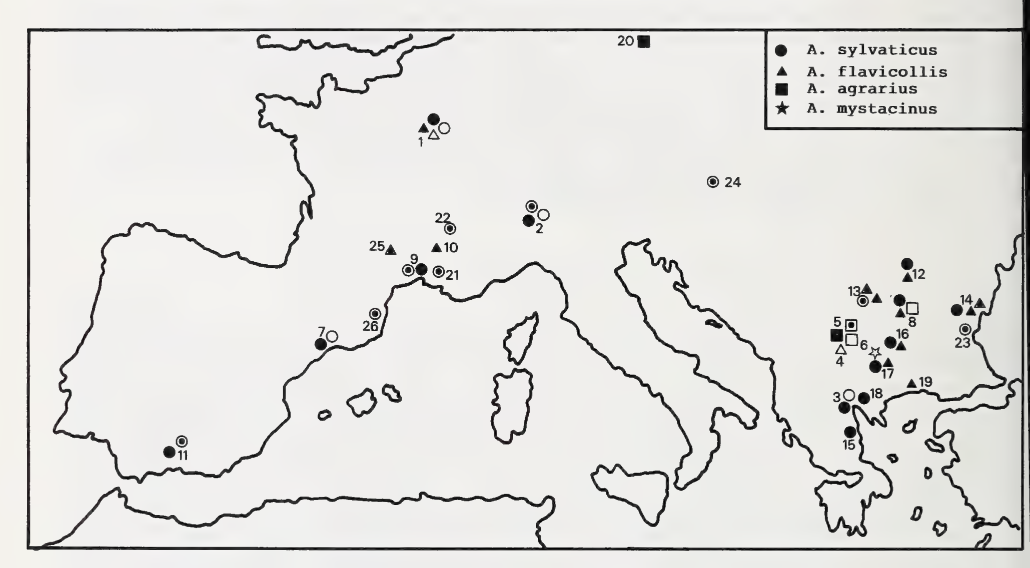


Fig. 1. Distribution of sampled localities and technique of analysis: empty symbols = allozymes; dark symbols = morphology; dotted symbols = chromosomes. Localities: France (1. St Cyr-les-Colons, 9. Gardiole, 10. Avène, 21. Mauguio, 22. Iseron, 25. Cuxac, 26. Banyuls); Italy (2. Ticino region near Pavia); Greece (3. Gallikos, 4. Strimonikon, 5. Doirani, 6. Prosotsani hills, 16. Aggitis river, 17. Prosotsani river, 18. University farm Thessaloniki, 19. Avas); Spain (7. Calonge, 11. Granada); Bulgaria (8. Plovdiv, 12. Karnobat, 13. Vrania, 14. General Toshevo, 23. Orizare); Germany (20. Lübeck) and Austria (24. Burgenland)

Morphological data were collected on specimens from France (1, 9, 10), Italy (2), Spain (7, 11), Bulgaria (8, 12, 13, 14), Greece (3, 15, 16, 17, 18, 19) and Germany (20).

The chromosomal study was performed on field mice from different localities: *A. sylvaticus* from France (9:1 male, 21:1 male, 22:1 female, 26:1 male), Spain (11:1 female), Bulgaria (13:1 female, 23:1 female) and Austria (24:1 female); *A. flavicollis* from France (25:1 female) and Bulgaria (14:1 male, 13:1 male); *A. agrarius* from Greece (4:1 male, 1 female). The karyotypes were established using the classical air-drying technique. No results were available for *A. mystacinus*.

In both the morphological and chromosomal study, all mice, except for *A. agrarius* and *A. mystacinus* which were unambiguously identified in the field, were ascribed to *A. sylvaticus* or *A. flavicollis* on the basis of their *LDH-2* alleles. The specimens are deposited as pickled carcasses at the Institut des Sciences de l'Evolution.

Table 1. **Allele frequencies at the 19 variable loci**

Locus		AS FR	AS IT	AS GR	AS SP	AF FR	AA GR	AA BU	AM GR
Adh	(N)	30	7	15	9	17	8	9	1
	f	0.62	0.50	0.70	0.72	0.00	1.00	1.00	0.00
	s	0.38	0.50	0.30	0.28	1.00	0.00	0.00	1.00
Gpd	(N)	33	10	24	10	19	8	9	1
	100	0.97	0.80	0.75	0.95	0.97	0.00	0.00	0.00
	70	0.02	0.05	0.25	0.05	0.00	0.00	0.00	0.00
	120	0.01	0.15	0.00	0.00	0.03	1.00	1.00	1.00
Alb	(N)	29	10	24	10	19	8	9	3
	100	1.00	1.00	1.00	1.00	0.00	0.00	0.00	1.00
	95	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00
	98	0.00	0.00	0.00	0.00	0.00	1.00	1.00	0.00
Amy-1	(N)	28	1	24	9	19	6	1	3
	a	0.98	1.00	0.02	0.22	0.03	0.00	0.50	0.00
	b	0.02	0.00	0.98	0.78	0.97	1.00	0.50	0.00
	c	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
Got-1	(N)	33	10	24	10	19	8	9	1
	100	0.97	1.00	1.00	1.00	1.00	0.00	0.00	1.00
	95	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	98	0.00	0.00	0.00	0.00	0.00	1.00	1.00	0.00
Gpi	(N)	30	10	24	9	16	8	9	3
	100	0.98	0.95	1.00	1.00	0.59	0.00	0.00	1.00
	80	0.02	0.00	0.00	0.00	0.41	0.00	0.00	0.00
	200	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00
	30	0.00	0.00	0.00	0.00	0.00	1.00	1.00	0.00
Hbb	(N)	19	7	24	6	2	8	9	3
	100	1.00	1.00	1.00	1.00	0.00	1.00	1.00	0.00
	120	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00
	140	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
Idh-1	(N)	33	10	24	9	19	8	9	1
	100	1.00	1.00	0.77	1.00	0.00	0.00	0.00	0.50
	120	0.00	0.00	0.23	0.00	1.00	0.00	0.00	0.00
	130	0.00	0.00	0.00	0.00	0.00	1.00	1.00	0.00
	125	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50
Ldh-1	(N)	33	10	24	10	19	8	9	3
	100	1.00	1.00	1.00	1.00	1.00	0.06	0.00	0.00
	90	0.00	0.00	0.00	0.00	0.00	0.94	1.00	0.00
	250	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
Ldh-2	(N)	33	10	24	10	19	8	9	1
	100	1.00	0.95	1.00	1.00	0.00	0.00	0.00	0.00
	115	0.00	0.00	0.00	0.00	1.00	0.00	0.00	1.00
	95	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00
	90	0.00	0.00	0.00	0.00	0.00	1.00	1.00	0.00
Ldr	(N)	22	7	23	9	19	8	9	3
	a	0.37	0.00	0.00	0.47	0.00	1.00	1.00	0.82
	b	0.63	1.00	1.00	0.53	1.00	0.00	0.00	0.18
Mdh-1	(N)	33	10	24	10	19	8	9	1
	100	1.00	1.00	1.00	1.00	1.00	0.00	0.00	1.00
	70	0.00	0.00	0.00	0.00	0.00	1.00	1.00	0.00
Mdh-2	(N)	33	10	24	10	19	8	9	1
	100	1.00	1.00	1.00	0.65	1.00	1.00	1.00	1.00
	80	0.00	0.00	0.00	0.35	0.00	0.00	0.00	0.00

Table 1 (continued)

Locus		Species / Locality *AS* FR	*AS* IT	*AS* GR	*AS* SP	*AF* FR	*AA* GR	*AA* BU	*AM* GR
Mod-1	(N)	33	10	24	10	19	8	9	1
	100	0.95	0.55	1.00	1.00	0.00	0.00	0.00	0.00
	110	0.05	0.40	0.00	0.00	0.00	0.00	0.00	0.00
	67	0.00	0.00	0.00	0.00	0.92	0.00	0.00	0.00
	30	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00
	90	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00
	50	0.00	0.00	0.00	0.00	0.00	1.00	1.00	0.00
	120	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
Np	(N)	31	10	24	10	18	8	9	3
	100	1.00	1.00	1.00	1.00	0.00	0.00	0.00	0.00
	80	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00
	90	0.00	0.00	0.00	0.00	0.00	1.00	1.00	0.00
	110	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
Pgd	(N)	31	10	24	10	18	8	9	3
	100	0.98	1.00	1.00	1.00	0.97	1.00	1.00	0.00
	110	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	70	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00
	130	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
Pgm	(N)	32	10	23	10	14	8	9	1
	100	0.79	1.00	1.00	1.00	1.00	0.50	0.67	0.50
	120	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	80	0.08	0.00	0.00	0.00	0.00	0.06	0.00	0.50
	70	0.00	0.00	0.00	0.00	0.00	0.44	0.33	0.00
Sdh	(N)	31	8	14	9	19	8	9	1
	100	0.98	1.00	1.00	1.00	1.00	0.00	0.00	0.00
	110	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	90	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
	80	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
	120	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00
Sod	(N)	33	10	24	10	19	8	9	1
	100	1.00	1.00	1.00	1.00	0.00	0.00	0.00	0.00
	70	0.00	0.00	0.00	0.00	1.00	0.00	0.00	1.00
	110	0.00	0.00	0.00	0.00	0.00	1.00	1.00	0.00

AS = *A. sylvaticus*; *AF* = *A. flavicollis*; *AA* = *A. agrarius*; *AM* = *A. mystacinus*. FR = France; IT = Italy; GR = Greece; SP = Spain; BU = Bulgaria.

Results

Genetic variability and differentiation

Genetic variability parameters (Table 2) were computed from the allelic frequencies (Table 1). Only one locus *(Idh-2)* was found monomorphic for the same allele in the four *Apodemus* species. Twelve loci (*Alb, Amy-1, Got-1, c+l.c, Hbb, Idh-1, Ldh-1, Ldh-2, Mdh-1, Pgd, Sdh* and *Sod*) discriminated at least two of the four species, whereas two loci were species diagnostic: *Mod-1* and *Np*.

All variability parameters were highest for *A. sylvaticus* (mean H = 0.08, mean $P_{0.05}$ = 21 % and mean A = 1.3) than for the other three species which ranged between 10 %–15 % for the rate of polymorphism and 4–6 % for mean heterozygosity. However, where sample sizes are small, this measure of variability may not be representative of the species as a whole.

Genetic distances (Table 3) calculated according to NEI (1978) were used to generate a UPGMA phenogram (Fig. 2). The latter agrees well with expectations in that *A. sylvaticus* and *A. flavicollis* cluster together, and both of these with *A. mystacinus*. *A. agrarius*, on the other hand is set well apart from the first three species, yielding a mean genetic distance of 1.28. Intraspecific genetic distances were computed for *A. sylvaticus* and *A. agrarius* only and yielded respectively a mean of 0.045 and 0.067 which falls within the value generally recorded for subspecific genetic differentiation.

Table 2. **Genetic variability measures**

Locality	N	A	P	H
A. sylvaticus				
France (1)	30	1.6	20	0.08
Italy (2)	9	1.3	25	0.08
Greece (3)	23	1.2	15	0.06
Spain (7)	9	1.3	25	0.09
Mean		*1.3*	*21*	*0.08*
A. flavicollis				
France (1)	17	1.3	10	0.04
A. agrarius				
Greece (5)	8	1.1	10	0.03
Bulgaria (8)	9	1.1	10	0.07
Mean		*1.1*	*10*	*0.05*
A. mystacinus				
Greece (6)	2	1.1	15	0.06

A = mean number of alleles; P = % of polymorphic loci (5 % level); H = mean heterozygosity (NEI 1978 except for *A. mystacinus* for which the sample size was too small). Numbers in parenthesis refer to localities.

Morphological discrimination

Morphological data are presented in Table 4 and Figure 3. Whereas discrimination of *A. agrarius* and *A. mystacinus* on morphological grounds is immediate, this is not the case between *A. sylvaticus* and *A. flavicollis* which show a large overlap in body lengths. Additionally, although the presence of a complete collar is species diagnostic, its absence is not since 35 % of the *A. flavicollis* we captured exhibited only a more or less large chest spot in lieu of a collar.

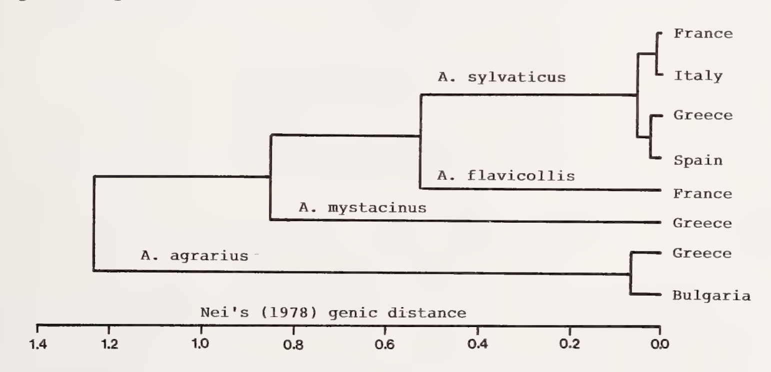


Fig. 2. UPGMA phenogram computed from genic distances

Chromosomal variability

The chromosomal analysis of specimens from each species corresponded to results from previous studies (KRAL 1970; SOLDATOVIĆ et al. 1975; BEKASOVA et al. 1980; ZIMA 1984). The karyotypes of *A. sylvaticus* and *A. flavicollis* both carried 48 acrocentric chromosomes except for the *A. flavicollis* from Bulgaria (14. General Toshevo) which had 49 chromosomes showing an additional small acrocentric chromosome. Such variation is common in this species and has been attributed to the presence of supernumerary chromosomes (SOLDATOVIĆ et al. 1975; ZIMA 1984; ZIMA and KRAL 1984). *A. agrarius* (2n

Table 3. **Genetic distance coefficients** (NEI 1978)

Locality	1	2	3	4	5	6	7	8
1. *AS*–FR	---							
2. *AS*–IT	0.016	---						
3. *AS*–GR	0.065	0.067	---					
4. *AS*–SP	0.039	0.063	0.022	---				
5. *AF*–FR	0.601	0.548	0.478	0.554	---			
6. *AA*–GR	1.236	1.284	1.115	1.107	1.446	---		
7. *AA*–BU	1.133	1.166	1.170	1.128	1.522	0.067	---	
8. *AM*–GR	0.876	0.866	0.932	0.908	0.823	1.532	1.512	---

AS = *A. sylvaticus*; *AF* = *A. flavicollis*; *AA* = *A. agrarius*; *AM* = *A. mystacinus*.
FR = France; IT = Italy; GR = Greece; SP = Spain; BU = Bulgaria.

Table 4. **Morphological data for samples of three *Apodemus* species**
Numbers after countries refer to localities sampled

Locality	N	BL (mm)	TL (mm)	HF (mm)	TL/BL	Chest spot No	Chest spot Sm	Chest spot L	Col
A. sylvaticus									
Italy (2)	10	93(3)	77(5)	22(1)	0.84(0.07)	20%	80%	–	–
Bulgaria (8. 12–14)	14	96(6)	81(4)	23(0)	0.86(0.05)	36%	57%	7%	–
Spain (7. 11)	9	93(5)	88(7)	22(1)	0.96(0.07)	44%	56%	–	–
Greece (3. 15–18)	48	107(2)	91(2)	23(0)	0.85(0.02)	81%	16%	3%	–
France (1)	33	84(2)	79(2)	21(1)	0.93(0.02)	33%	39%	27%	
(9)	20	97(2)	84(3)	21(1)	0.87(0.03)	30%	70%	–	–
Mean		*97(2)*	*84(1)*	*22(0)*	*0.88(0.01)*	*53%*	*39%*	*8%*	–
A. flavicollis									
Greece (16–17)	2	97(–)	88(–)	23(–)	0.92(–)	–	100%	–	–
Bulgaria (8. 12–14)	6	98(7)	86(1)	22(2)	0.88(0.08)	–	75%	–	25%
France (10)	20	94(5)	95(4)	23(1)	1.03(0.04)	–	15%	35%	50%
(1)	19	94(5)	99(5)	24(0)	1.06(0.03)	–	–	5%	95%
Mean		*95(3)*	*95(3)*	*23(0)*	*1.01(0.03)*	–	*19%*	*16%*	*65%*
A. agrarius									
Greece (5)	8	112(5)	78(2)	22(1)	0.69(0.02)				
Germany (20)	6	102(5)	70(12)	19(1)	0.69(0.17)				
Mean		*108(4)*	*75(5)*	*21(1)*	*0.69(0.05)*				

BL = body length; TL = tail length; HF = hind foot length; chest spot color: no, small (Sm) or large (L) spot; Col = complete collar. STandard errors in parenthesis.

= 48) showed four pairs of small metacentric chromosomes which increased the NF to 56. No other chromosomal variability was found within samples.

Discussion

Interspecific genetic differentiation at 20 loci is presented for four species of the genus *Apodemus*. Previous studies on these same species were made by GEMMEKE (1980) but the electrophoretic survey included only 11 loci. More recent and extensive work was performed by NASCETTI and FILIPPUCCI (1984) on 27 loci but was restricted to the subgenus *Sylvaemus*. The overview of these three independent studies shows that the

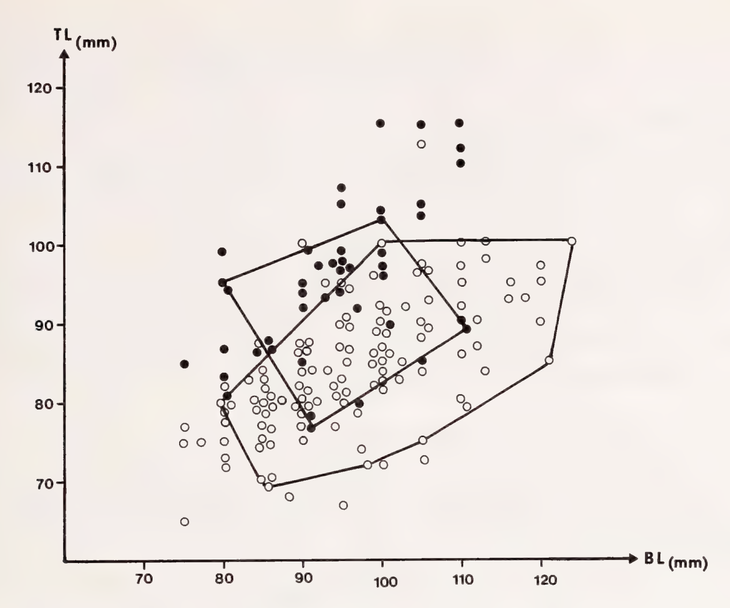


Fig. 3. Body (BL) and tail length (TL) distribution. Empty circle = *A. sylvaticus;* dark circle = *A. flavicollis.* Envelopes show the morphological variability of samples from Bulgaria and Greece for both species

overall specific discrimination (the number of diagnostic loci between two species) is similar and often more important with the set of loci and the electrophoretic buffers we used. This reasoning is based on the assumption that the differences in scoring results are probably more related to the techniques used than to variability of the biological material. These differences in discriminating capacity do not, however, alter the phylogenetic relationships as determined by the genetic distances.

Our results agree with previous work on this genus (Gemmeke 1980) in that *A. sylvaticus, A. flavicollis* and *A. mystacinus* belonging to the same subgenus *Sylvaemus* cluster together whereas *A. agrarius*, which represents a different subgenus *(Apodemus)* is exterior to this group.

That morphological discrimination is difficult and even impossible between specimens of *A. sylvaticus* and *A. flavicollis* inhabiting Southern Europe has previously been shown for France (Benmehdi et al. 1980), Italy (Nascetti and Filippucci 1984) and Germany (Engel et al. 1973; Gemmeke 1980) and is here extended to Bulgaria and Greece. Previous results are here again confirmed in that in all cases of morphological ambiguity, the biochemical analysis allowed to assign the specimens to either species and showed the absence of any introgression between them. It is therefore suggested that field specimens be identified by electrophoretic methods (on albumin for example, Debrot and Mermod 1977; Gemmeke 1981) or by using the morphological criteria put forth by Filippucci et al. (1984) which enabled to discriminate at least 95 % of Italian specimens and should be tested elsewhere.

This study shows that the separation of the four *Apodemus* species studied into two subgenera is supported by the biochemical distance data. Within the subgenus *Sylvaemus*, *A. sylvaticus* and *A. flavicollis* are remarkable in that they represent morphologically and chromosomally very similar species with relatively large genic distances.

The particular position of *A. agrarius* is worth commenting on, however. The very important genic distance between this species and those of the subgenus *Sylvaemus* is

probably an underestimate, being at the limit of the discriminating power of electrophoretic methods. In fact, ISKANDAR and BONHOMME (1984) showed that sequential electrophoresis allowed to uncover 27 % more alleles between the two subgenera whereas no additional variation was revealed between the three species of the subgenus *Sylvaemus*. These data then suggest that *A. agrarius* is probably even more distantly related to the *Sylvaemus* species group than what we indicate herein. Based on these data, we agree with BONHOMME et al. (1985) in suggesting that a taxonomic revision of this group be made. It is probable that the two current subgenera will be elevated to a genus rank since *Apodemus* appeared not to be more closely related to *Sylvaemus* than to other murid (BONHOMME et al. 1985) or even arvicolid (data not based on sequential electrophoresis: GILL et al. 1987) genera. For this analysis, it would be imperative that biochemical data be collected for species belonging to the third subgenus *(Alsomys)* in order to correctly establish the evolutionary relationships within the *Apodemus* complex.

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Zusammenfassung

Genetische Differenzierung bei vier Apodemus-Arten in Südeuropa: A. sylvaticus, A. flavicollis, A. agrarius und A. mystacinus (Muridae, Rodentia)

Die genetische Variabilität von vier südeuropäischen *Apodemus*-Arten wurde durch Elektrophorese von Proteinen geschätzt, die über 20 Genloci kodiert werden. Die nach NEI (1978) berechneten Abstandswerte entsprechen ungefähr den bisherigen Vorstellungen von der abgestuften Verwandtschaft dieser Arten. So unterscheidet sich *A. agrarius* (Untergattung *Apodemus*) beträchtlich von den drei anderen, in der Untergattung *Sylvaemus* zusammengefaßten Arten. *Apodemus sylvaticus* und *A. flavicollis* überschneiden sich in ihren morphologischen Merkmalen in Südeuropa stark, lassen sich aber gelelektrophoretisch stets einwandfrei bestimmen. Alle vier Arten haben gewöhnlich 48 Chromosomen. Nur 1 *A. flavicollis* von 27 aus Bulgarien hatte mit einem kleinen zusätzlichen akrozentrischen Element insgesamt 49 Chromosomen.

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Cranial infraspecific differentiation in *Proechimys iheringi* Thomas (Rodentia: Echimyidae)

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Abstract

Proechimys iheringi Thomas is an echimyid rodent occurring in eastern Brazil from the states of Bahia to São Paulo. MOOJEN (1948) recognized six subspecies of *P. iheringi* primarily on the basis of clinal variation in the number of cheekteeth counterfolds. In this study we analyzed infraspecific differentiation in 13 morphometric cranial characters in three populations assignable to three subspecies of *P. iheringi*. Cranial dimensions vary clinally increasing from north to south and morphometric differentiation is correlated with geographic distance. The congruence between the clinal variation in cheekteeth counterfolds and cranial traits indicates that the trinomial nomenclature should not be applied to *P. iheringi*.

Introduction

Proechimys iheringi Thomas is an echimyid rodent which occurs in eastern Brazil, ranging from Bahia to São Paulo (MOOJEN 1948). In a detailed analysis of infraspecific differentiation in *P. iheringi* MOOJEN (1948) detected variation in several skull traits including incisive foramen, tympanic bulla, mesopterigoid fossa, palatine foramen, and vomerine sheath. In spite of the variation in these characters, MOOJEN (1948) relied primarily on the number of cheekteeth counterfolds, which varies clinally increasing from north to south, to recognize six subspecies in *P. iheringi*, namely *P. i. denigratus* from Bahia, *P. i. gratiosus*, *P. i. paratus*, and *P. i. panema* from Espirito Santo, *P. i. bonafidei* from Rio de Janeiro, and *P. i. iheringi* from São Paulo (Fig. 1). The subspecific structure in *P. iheringi* is thus based on a trait that varies on a cline and whose differentiation is correlated with geographic distance (MOOJEN 1948).

In this paper, we analyzed cranial variation in three populations of *P. iheringi* assignable to the following subspecies: *P. i. denigratus*, *P. i. gratiosus*, *P. i. bonafidei* from the states of Bahia, Espírito Santo, and Rio de Janeiro, respectively. The primary objective of this study was to determine whether the pattern of differentiation in cranial quantitative traits is congruent with the clinal variation in cheekteeth counterfolds and to address the question of recognition of infraspecific units in *P. iheringi*.

Material and methods

A total of 54 specimens of *P. iheringi* available in the mammal collection of the Museu Nacional (Rio de Janeiro) was examined in this study. All specimens were classified to one of the 10 age categories defined by PATTON and ROGERS (1983) for *P. brevicauda* on the basis of tooth eruption and occlusal surface wear criteria. This procedure was employed in order to control the ontogenetic source of variation, and 42 specimens from age classes 8–10 were selected for the analysis of geographic variation because they were adults by the criteria of PATTON and ROGERS (1983).

The specimens analyzed in this study represent samples collected at the following localities: Ilhéus, state of Bahia (13° 01′ S, 40° 01′ W; n = 16), Santa Tereza, state of Espírito Santo (19° 55′ S, 40° 36′ W;

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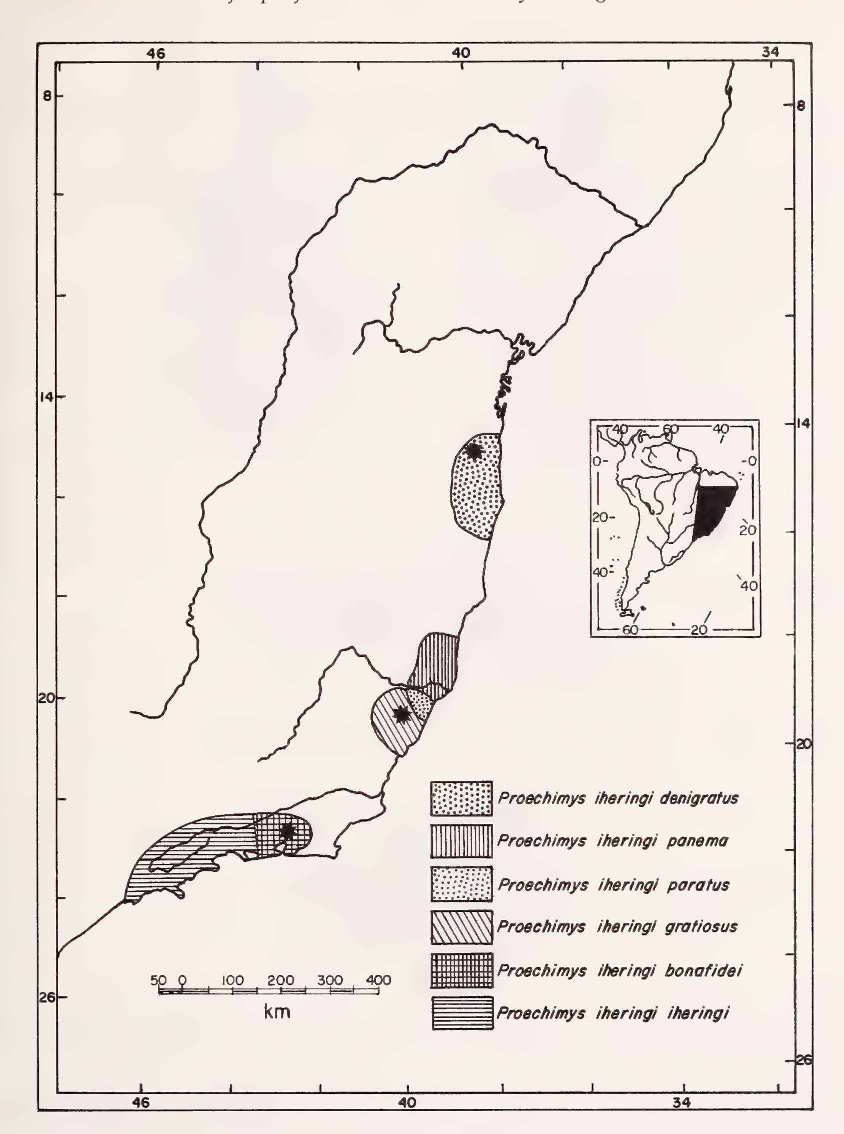


Fig. 1. Ranges for the subspecies of *Proechimys iheringi* Thomas according to Moojen (1948). The stars denote locality samples analyzed in this study

n = 18) and Teresópolos, state of Rio de Janeiro (22° 26′ S, 42° 36′ W; n = 8). Sexes were pooled in the analysis of geographic variation to increase sample sizes.

Twelve cranial measurements defined in Patton and Rogers (1983) in addition to one mandibular measurement were taken with electronic digital calipers accurate to 0.01 mm, as follows: palatal length A (PL), zygomatic breadth (ZB), nasal length (NL), interorbital constriction (IC), rostral breadth (RB), diastema length (DL), rostral depth (RD), skull length (SL), basal length (BL), rostral length (RL), maxillary breadth (MB), pospalatal length (PP), and mandibular length (ML) (Fig. 2).

Cranial character variation in *P. iheringi* was analyzed by univariate and multivariate procedures (Sokal and Rohlf 1981; Neff and Marcus 1980). Cranial characters were tested for significant differences among localities by univariate analysis of variance (anova). Significant characters were tested for maximally non-significant subsets of means employing Ryan-Einot-Gabriel-Welsch (regwf) test on the main effect represented by the variable locality.

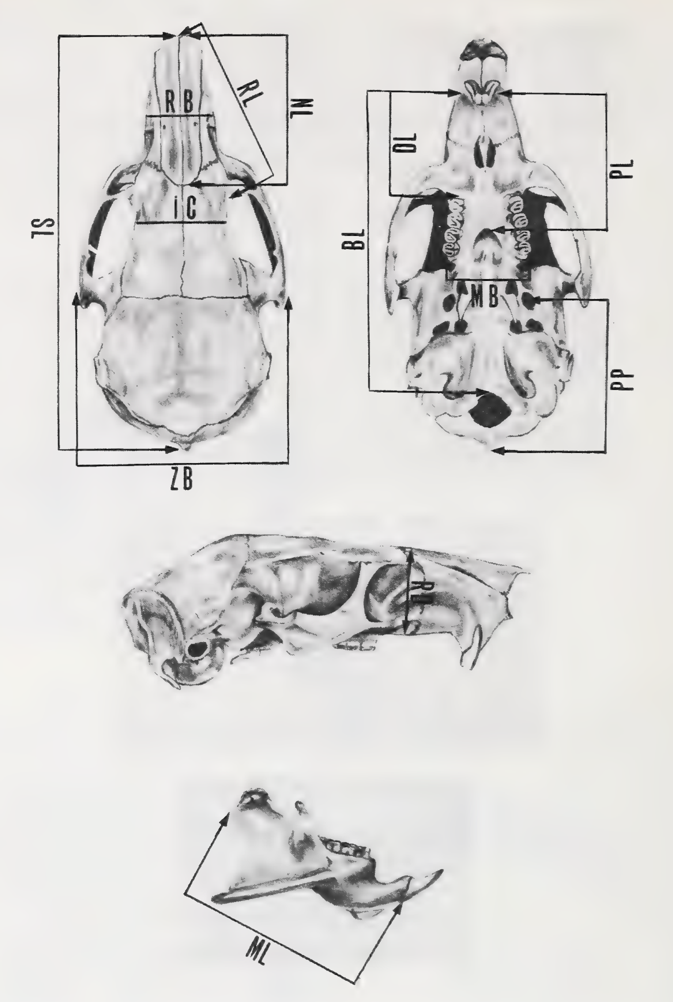


Fig. 2. Thirteen measurements taken on the skulls of *Proechimys iheringi* Thomas (see text for explanation of measurement abbreviations)

The pattern of variation in multivariate character space was analyzed by principal components analysis (Neff and Marcus 1980) and size-independent canonical discriminant analysis (Strauss 1985). The first pooled among-group principal component was used to study size variation among populations of *P. iheringi*. Scores derived from the first principal component were used as a measure of individual overall cranial size and were tested by univariate anova for heterogeneity among the populations.

Size-independent canonical discriminant analysis was employed to analyze patterns of discrimination and ordination among the *P. iheringi* populations. This procedure removes the effect of size variation within groups by performing canonical discriminant analysis on the residuals obtained from the regressions of each log-transformed character separately on the first pooled within-group principal component (Strauss 1985). This procedure was employed because *P. iheringi* shows post-ontogenetic growth (indeterminate growth) that generates size variation within populations (Pessôa 1989) that may confound the analysis of geographic variation (Thorpe 1983). Scores derived from canonical discriminant analysis were plotted to assess the pattern of ordination and discrimination among the populations of *P. iheringi*. Canonical loadings were expressed as bivariate correlations calculated between original character values and scores on the canonical variates (Strauss 1985).

Statistical analyses were performed using SAS-PC Version 6, the current microcomputer edition of the Statistical Analysis System (SAS Institute, 1988).

Results

All cranial characters, except for palatal length and diastema length, increase in mean size from north to south, i.e. from the state of Bahia to the state of Rio de Janeiro (Table 1). Univariate analysis of variance indicates that all cranial traits differ significantly in the three populations of *P. iheringi* (Table 1). Nevertheless, the pattern of inter-locality differentiation in cranial traits is not uniform as indicated by the REGWF procedure (Table 1). Cranial

Table 1. **Standard statistics for 13 cranial characters (in mm) in three populations (BA, ES, and RJ) of *Proechimys iheringi* Thomas**

Character	Mean (SD)	Mean (SD)	Mean (SD)	F	P
Palatal length	ES 15.82 (0.79)	BA 16.30 (0.79)	RJ 16.80 (0.76)	4.35	0.0201
Zygomatic breadth	BA 24.02 (1.21)	ES 25.32 (1.12)	RJ 26.08 (1.18)	9.58	0.0004
Nasal length	BA 15.91 (0.98)	ES 17.47 (0.99)	RJ 19.33 (1.27)	28.41	0.0001
Interorbital constriction	BA 11.06 (0.57)	ES 11.53 (0.96)	RJ 12.47 (0.55)	9.50	0.0005
Rostral breadth	BA 7.03 (0.58)	ES 7.36 (0.58)	RJ 8.26 (0.43)	12.97	0.0001
Diastema length	ES 10.16 (0.80)	RJ 10.98 (0.63)	BA 11.15 (0.78)	7.38	0.0020
Rostral depth	BA 9.36 (0.52)	ES 10.05 (0.83)	RJ 10.87 (0.63)	13.21	0.0001
Skull length	BA 46.27 (1.81)	ES 49.89 (2.31)	RJ 53.00 (2.66)	26.87	0.0001
Basal length	BA 34.74 (1.67)	ES 34.84 (1.55)	RJ 37.22 (1.57)	7.30	0.0022
Rostral length	BA 19.39 (0.99)	ES 21.43 (1.71)	RJ 23.28 (1.35)	22.26	0.0001
Maxillary breadth	BA 8.17 (0.42)	ES 8.45 (0.88)	RJ 9.09 (0.51)	5.28	0.0096
Pos-Palatal length	BA 2.72 (0.75)	ES 23.40 (0.94)	RJ 24.58 (1.26)	27.20	0.0001
Mandibular length	BA 23.87 (1.23)	ES 24.70 (1.38)	RJ 26.20 (1.54)	7.87	0.0014

Statistics given are mean, standard deviation, F-value of an analysis of variance and associated probability levels (P), and results of REGWF analysis. Lines below population means connect nonsignificant subsets. BA = Bahia, ES = Espirito Santo, and RJ = Rio de Janeiro.

characters such as interorbital constriction, rostral breadth, basal length, maxillary breadth, and mandibular length are not significantly different in the populations of Bahia and Espírito Santo, although individuals in both populations are significantly smaller than those in the population from Rio de Janeiro. The three populations differ statistically in several cranial traits including nasal length, rostral depth, skull length, rostral length, and pos-palatal length. Palatal length, zygomatic breadth, and diastema length have unique patterns of variation among the three populations (Table 1).

In order to analyze size variation among populations of *P. iheringi* in multivariate character space, the first pooled among-group principal component (PAGPC-1) was extracted from the covariance matrix of log-transformed character values. PAGPC-1 can be interpreted as a general size factor since all vector coefficients are positive and have significant correlations with log-transformed character values (STRAUSS 1985) (Table 2). The scores from principal components analysis for the individuals in the three populations of *P. iheringi* can then be used as a measure of multivariate cranial size. Mean score values increase from north to south in the populations of Bahia (−0.0729), Espírito Santo (0.0056), and Rio de Janeiro (0.1163) and these mean values were shown to be highly significant different by an univariate ANOVA ($F = 16.48$; $P < 0.0001$).

The pattern of ordination and discrimination of *P. iheringi* populations was assessed by

Table 2. **Principal component and canonical variate loadings for 13 cranial morphometric characters in *Proechimys iheringi* Thomas**

Character	PAGPC-1	r	CV-1	CV-2
Palatal length	0.160	0.709**	0.845**	0.067ns
Zygomatic breadth	0.212	0.852**	−0.083ns	−0.416*
Nasal length	0.380	0.935**	−0.650**	0.238ns
Interorbital constriction	0.134	0.935**	−0.652**	0.205ns
Rostral breadth	0.339	0.816**	−0.053ns	0.341*
Diastema length	0.178	0.510*	0.966**	0.002ns
Rostral depth	0.357	0.932**	−0.253ns	−0.116ns
Skull length	0.285	0.952**	−0.764**	−0.078ns
Basal length	0.193	0.846**	0.590**	0.201ns
Rostral length	0.401	0.960**	−0.709**	−0.132ns
Maxillary breadth	0.306	0.798**	0.211ns	−0.050ns
Pos-Palatal length	0.242	0.889**	−0.667**	−0.045ns
Mandibular length	0.247	0.900**	0.349*	−0.153ns
Percent of variance explained	73.71		89.79	10.21

Canonical variate loadings are expressed as vector correlations between log-transformed character values and canonical scores. PAGPC-1 is the pooled among-group first principal component. r is the Pearson product-moment correlation coefficient between cranial characters and the first principal component. * $P<0.05$; ** $P<0.0001$; n = non significant

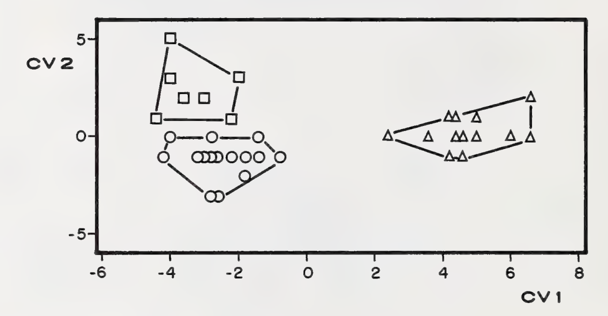


Fig. 3. Scatterplot of individual scores from a size-independent canonical discriminant analysis from three populations of *Proechimys iheringi*. Bahia (triangles), Espírito Santo (circles), and Rio de Janeiro (squares)

size-independent canonical discriminant analysis. The first canonical variate (CV-1) explains 89.79 % of the total among-group variation while CV-2 accounts for the remaining 10.21 %. The plot of canonical variate scores shows that the three populations of *P. iheringi* occupy different positions in the reduced space of canonical variates (Fig. 3). The population from Bahia is discriminated from the populations from Espírito Santo and Rio de Janeiro along CV-1, whereas individual scores for the latter populations have non-overlapping distributions along CV-2. Figure 3 also indicates that the populations from Espírito Santo and Rio de Janeiro, which are the geographically closest, are also morphometrically more similar. These populations are more differentiated morphometrically from the population of Bahia which is geographically farther.

The vectors of correlations between canonical variates and original log-transformed character values indicate that the population from Bahia differs from those of Espírito Santo and Rio de Janeiro in most cranial measures of length (Table 2). Canonical variate 1 correlations indicate a contrast between palatal length, diastema length, basal length, and mandibular length with positive significant correlations and nasal length, interorbital

constriction, skull length, rostral length, and pos-palatal length with negative significant correlations. On the other hand, the population from Espírito Santo differs from that of Rio de Janeiro in zygomatic breadth with a negative significant correlation and rostral breath with a positive significant correlation (Table 2).

Discussion

The univariate statistical analysis of cranial character variation did not produce a consistent pattern of inter-locality population differentiation in *P. iheringi*, although most characters vary in a cline increasing in size from north to south. The lack of consistency in character trends observed for *P. iheringi* in this study is a common result, whenever morphometric characters are analyzed univariately (Baker 1980; Thorpe 1983; Macêdo and Mares 1987).

The multivariate procedures employed produced a much clearer picture of the nature and extent of inter-locality differentiation in *P. iheringi*. Multivariate cranial size, estimated by mean score values derived from principal components analysis, increases from north to south confirming the cline observed for most cranial morphometric traits in *P. iheringi* in the univariate analysis. This cline follows the same direction of the gradient in cheekteeth counterfolds observed by Moojen (1948). The pattern of ordination of *P. iheringi* populations in the space of canonical variates further indicates a correlation between morphometric and geographic distance confirming Moojen's (1948) observations based on qualitative arguments.

The analysis of geographic differentiation in *P. iheringi* reported in this paper is based upon population samples representing three subspecies among the six forms recognized by Moojen (1948). We believe nevertheless that our findings are representative of the overall pattern of variation in *P. iheringi* since the three subspecies we analyzed are distributed over most of the range of this species (Fig. 1). Our results, in addition to Moojen's (1948) findings, indicate that the variation in *P. iheringi* is geographically structured in a cline of increasing cranial dimensions and number of cheekteeth counterfolds from northern to southern populations. The recognition of subspecies on the basis of clinal variation, as is the case for *P. iheringi*, has been criticized primarily due to the continuous nature of the variation expressed in a cline (Barrowclough 1982; Thorpe 1987). The validity of the recognition of subspecific units in *P. iheringi* can be questioned since the application of trinomials has been considered suitable to describe character variation that do not simply form clines but rather diagnoses groups of populations indicating the existence of independent infraspecific units (Barrowclough 1982; Thorpe 1987; Smith and Patton 1988; Patton and Smith 1989).

Our preliminary study indicates that, on the basis of the pattern of cranial variation, the use of the subspecific nomenclature is not justified for *P. iheringi*. Nevertheless, other character systems should be surveyed to assess the nature and structure of variation in order to understand the process of differentiation in this species and determine whether independent evolutionary units (sensu Smith and Patton 1988; Patton and Smith 1989) should be recognized for *P. iheringi*.

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Zusammenfassung

Intraspezifische Schädelvariabilität bei Proechimys iheringi Thomas (Rodentia: Echimyidae)

Schädel von Igelratten *(Proechimys iheringi)* aus drei Populationen, die drei der sechs beschriebenen Unterarten dieser Art zuzuordnen sind, wurden in 13 Maßen verglichen. Danach nimmt die Schädelgröße von Norden nach Süden zu. Die allgemeinen morphometrischen Abstände zwischen den Populationen sind mit ihren geographischen Abständen korreliert. Da sich auch die Zahl der Schmelzfalten in gleicher Richtung klinal ändert, läßt sich eine Gliederung von *Proechimys iheringi* in Unterarten mit diesen Merkmalen nicht rechtfertigen.

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Thermoregulation and torpor in African woodland dormice, *Graphiurus murinus*, following cold acclimation

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Abstract

Studied thermoregulation of 3 adult woodland dormice *(Graphiurus murinus)* following acclimation to 15 °C and 10 °C. The dormice entered hibernation under these conditions characterised by a fall in body temperature to within 1 °C of ambient, and a prolonged reduction in oxygen consumption measured over 24 h at 10 °C and 5 °C. Non-shivering thermogenic capacity exceeded that required to re-attain homeothermy by 20 %, but would permit these dormice to maintain normothermia down to −5 °C. The cycle of body mass displayed by *G. murinus* in the present study is characteristic of hibernating temperate dormice, but was not observed in specimens collected throughout the year in southern Africa. It therefore appears that woodland dormice may not enter hibernation throughout their distribution during winter, but may exhibit facultative torpor under adverse climatic conditions.

Introduction

African woodland dormice, *Graphiurus murinus,* are small, arboreal rodents found throughout large areas of tropical and subtropical Africa (Smithers 1983). Although Eisentraut (1962) could not elicit torpor in *G. murinus* from West Africa (Cameroon), Smithers (1983) suggested that this species shows signs of lethargy during cold weather in South Africa. Following the discovery of a torpid woodland dormouse during rodent trapping by the authors outside Pretoria in March 1987, the following study was initiated to investigate thermoregulation and torpor in *G. murinus* under controlled laboratory conditions.

Material and methods

Three African woodland dormice (2 adult females, 1 adult male) were collected at Vaalkop Dam Nature Reserve (25° 23′ 27° 28′ E) during April 1989. Within one week of capture the dormice were transferred to a windowless climate chamber (Specht Scientific, Johannesburg) at Pretoria University (25°45′ S 28°12′ E) wherein photoperiod and temperature could be accurately controlled. Throughout the study the photoperiod within the chamber was maintained at 10 h light : 14 h dark (lights on at 07h00 and off at 17h00) which closely resembled the photoperiod prevailing at Vaalkop Dam during mid-winter. The dormice were initially acclimated for 50 days at an ambient temperature (T_a) of 15 °C followed by a further 50 days at T_a = 10 °C. The dormice were housed separately in standard laboratory rat cages containing sawdust, shredded paper and a 500 ml plastic beaker which served as a nest box. Water, sunflower seeds, rat cubes and rabbit pellets (Epol, Vereniging) were provided ad libitum, a diet occasionally supplemented with pieces of fresh apple.

The body mass of each dormouse was recorded upon capture and subsequently at regular intervals throughout the study. In addition, rectal temperatures (T_b) were measured between 07h00–13h00 on five occasions during acclimation to both T_a = 15 °C and T_a = 10 °C. T_b was determined by inserting a chromel alumel thermocouple (K-Type: Fluke, Everett), attached to a digital thermometer, approximately 2 cm into the rectum for a period not exceeding 15 sec. To avoid undue perturbation, body mass and rectal temperature were recorded at intervals of 3 days or more, and at all other times the dormice remained undisturbed within the climate chamber.

Following 50 days acclimation at 10 °C the oxygen consumption ($\dot{V}O_2$) of the dormice was measured as an indication of metabolic rate (MR) using an open-circuit system (as described by Depocas and Hart 1957, and Hill 1971). The dormice were placed in perspex metabolic chambers

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through which a flow of dried air (Silica Gel: Holpro, Johannesburg) was passed at a rate of 600 ml × min^{-1}. The chambers were immersed in a constant temperature water bath (Labotec, Isando), and a chromel alumel thermocouple within the chamber was used for monitoring chamber temperature (T_c). Following full equilibration $\dot{V}O_2$ was recorded using an Ametek S–3A/I oxygen analyser (Applied Electrochemistry, Pittsburgh) linked to a multi-channel data logger (Grant Instruments, Chambridge). The oxygen analyser was calibrated before and after measurement, and $\dot{V}O_2$ was corrected to standard temperature and pressure, dry (STPD).

Average daily metabolic rate (ADMR) was measured over 48 h in large (13 l) metabolic chambers. The dormice were transfered to these chambers, together with their bedding and food, 20 h prior to the start of measurement, and were subsequently subjected to 24 h at T_c = 10 °C followed by 24 h at T_c = 5 °C. Air leaving the chambers was connected to a three-way valve and time-switch (Air/Water 350 KPA: Ascoreg, Johannesburg), so that $\dot{V}O_2$ from two dormice could be monitored simultaneously every 30 min using a single oxygen analyser. At the end of measurement the mass and rectal temperature of each dormouse was recorded.

Resting metabolic rate (RMR) was measured following one hour's exposure to T_c = 5 °C and 10 °C within smaller metabolic chambers (700 ml). $\dot{V}O_2$ was monitored over 30 min after which rectal temperature and body mass were recorded.

Maximum oxygen consumption ($\dot{V}O_{2max}$) following an injection of noradrenaline (NA) was used as an indication of non-shivering thermogenetic capacity (as described by Heldmaier 1971). The dormice were anaesthetised with sodium pentobarbitone (70 mg/kg intraperitoneally. Sagatal: May-baker, Port Elizabeth) after which a chromel alumel thermocouple (J-Type: Grant Instruments, Cambridge) was inserted deep into the rectum to measure T_b and secured to the base of the tail with tape. Following a subcutaneous injection of 1.5 mg/kg NA (Heldmaier 1971) the dormice were transfered to a small metabolic chamber (700 ml) at T_c = 30 °C and $\dot{V}O_2$ and T_b were recorded simultaneously at one minute intervals for 60 min using the multichannel data logger. $\dot{V}O_{2max}$ and T_{bmax} were taken as the highest values of $\dot{V}O_2$ and T_b recorded following NA injection.

All results are presented as mean ± one standard deviation unless otherwise stated.

Results

Body mass

Following acclimation, the mean body mass of dormice in the present study entered a cycle comprising a rapid period of weight gain followed by a slower sequence of weight loss. From a mean capture mass of 29.1 ± 4.3 g the dormice weighed 43.2 ± 4.3 g after 25 days in captivity, an increase of almost 50 %. Following a gradual decline the dormice returned to capture mass by Day 65, after which they retained a stable mean body mass for the remainder of the study.

Body temperature

All the measurements of T_b taken during acclimation to T_a = 15 °C and 10 °C were pooled and displayed in two histograms (Fig. 1). Under both T_a regimes the dormice were predominantly torpid, with the majority of T_b measurements falling at, or slightly above T_a. At these T_bs the dormice were stiff and displayed the lack of responsivity and coordination characteristic of deep torpor. In addition, the level of hypothermia recorded was dependant upon T_a, being lower at T_a = 10 °C than at T_a = 15 °C. Few T_b measurements fell within the normothermic range for mammals (33 °C–36 °C) which suggests that the dormice were usually in torpor between 07h00 and 13h00 when T_b was recorded.

Metabolism

At 10 °C the mean RMR of the dormice was 3.74 ± 0.14 $mlO_2 \times g^{-1} \times h^{-1}$ (T_b = 34.7 ± 0.4 °C) and increased slightly at 5 °C to 3.99 ± 0.15 $mlO_2 \times g^{-1} \times h^{-1}$ (T_b = 34.1 ± 0.1 °C). In contrast, $\dot{V}O_2$ measured over 24 h at these temperatures remained at low levels for prolonged periods, punctuated with brief increases in $\dot{V}O_2$ lasting between 1 h and 6 h (Fig. 2). Excluding these incidents of increased metabolism, the mean ADMR

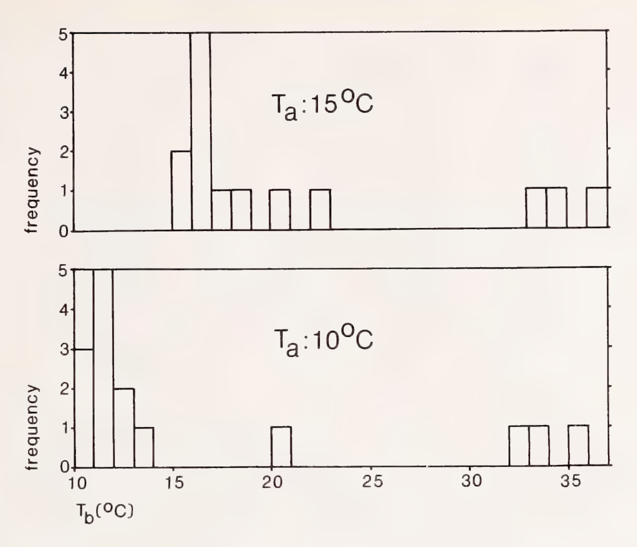


Fig. 1. Rectal temperatures recorded between 07h00 and 13h00 during acclimation to T_a = 15 °C and 10 °C

at 10 °C (0.27 ± 0.06 $mlO_2 \times g^{-1} \times h^{-1}$) was only 7.3 % RMR and at 5 °C (0.52 ± 0.26 $mlO_2 \times g^{-1} \times h^{-1}$) was 13.0 % RMR (Fig. 3). Despite the modest rise in ADMR following exposure to 5 °C, the dormice exhibited a mean T_b of 6.0 ± 0.3 °C at the end of measurement.

The male dormouse died under anaesthesia during the measurement of NST, whilst the females displayed a mean $\dot{V}O_{2max}$ of 5.75 ± 0.67 $mlO_2 \times g^{-1} \times h^{-1}$ following NA injection, accompanied by mean T_{bmax} of 40.6 ± 1.0 °C. When compared to ADMR and RMR in Fig. 3 $\dot{V}O_{2max}$ was found to exceed the level of heat production required to maintain normothermia at either 10 °C or 5 °C. However, according to HELDMAIER's (1971) allometric equation relating $\dot{V}O_{2max}$ to body mass, the $\dot{V}O_{2max}$ recorded in the present study is approximately 90 % of that predicted for mammals of similar body size following cold (5 °C) exposure ($\dot{V}O_{2max}$ predicted: 6.37 $mlO_2 \times g^{-1} \times h^{-1}$).

Discussion

The results of the present study clearly indicate that *G. murinus* from southern Africa is capable of spontaneous bouts of deep torpor when confronted with cold stress under simulated winter photoperiod. Furthermore, these bouts of torpor exceeded 24 h in duration, which suggests that *G. murinus* entered hibernation under these conditions. Hibernating dormice rarely arouse when challenged with declining temperatures and instead increase metabolic thermogenesis to maintain T_b at non-lethal levels even as T_a falls to 0 °C or below (WALHOVD 1976; PAJUNEN 1986). In the present study torpid dormice displayed an increase in metabolism when T_a fell from 10 °C to 5 °C, which indicates that torpor in *G. murinus,* in common with other dormice, is facultative and under strict thermoregulatory control. However, a consequence of this increase in metabolic rate is that an optimal T_a exists for maximum energy savings during hibernation, as described for the garden dormouse, *Eliomys quercinus* (PAJUNEN 1986). For *G. murinus* the optimal T_a appears to fall between 10 °C and 5 °C which corresponds to the mean night-time temperature of around 5 °C prevailing during winter (June/July) at Vaalkop Dam (Pretoria Weather Bureau: Brits Met. Stn. 25°35′ S 27°49′ E 1939–1984).

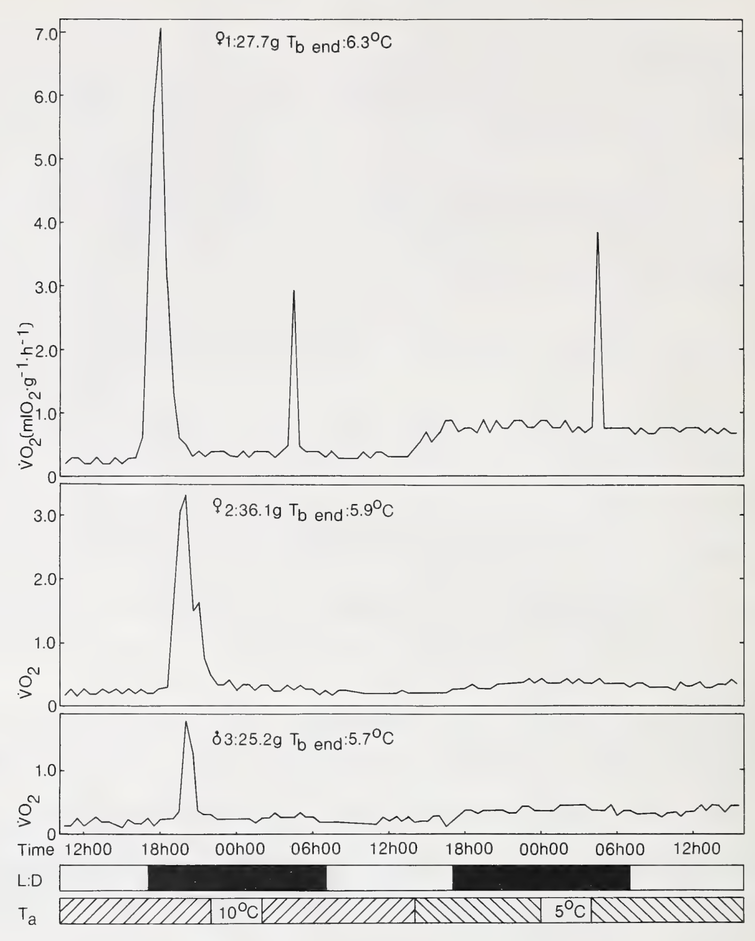


Fig. 2. Oxygen consumption ($\dot{V}O_2$) of 3 *Graphiurus murinus* measured over 24 h at 10 °C and 5 °C

Non-shivering thermogenesis is the dominant pathway for heat production in small mammals (Böckler et al. 1988) although hibernators exhibit higher levels of NST than euthermic species of similar body size even in the absence of cold adaptation (Janský 1973). This enhanced capacity for NST amongst hibernators is believed to be associated with the heat required for arousal from hypothermia (Abbotts and Wang 1980). If we assume that the specific heat capacity of animal tissue is 3.4 $kJ \times g^{-1}$ (Chappell and Bartholomew 1981) and that the calorific equivalent of oxygen is 20.1 $J \times mlO_2^{-1}$ (Schmidt-Nielsen 1983) then rewarming a 31.9 g dormouse from T_b = 6.1 °C to 34.4 °C (28.3 °C) in the present study would require 3.07 kJ or 152.74 mlO_2. This compares with the total heat produced during NST of 5.75 $mlO_2 \times g^{-1} \times h^{-1}$ or 183.43 $mlO_2 \times h$, which exceeds that required for rewarming by 20 %. For this reason NST in *G. murinus* may be important not only for arousal from hypothermia, but also for the maintenance of homeothermy in the cold. In this context the lowest T_a at which *G. murinus* can thermoregulate, using NST alone, can be calculated assuming that Newton's law of cooling holds for this species as proposed by Scholander et al. (1950): (Thermal conductance below themoneutrality $[C_m] = \dot{V}O_2 \times [T_b - T_a]^{-1}$). Based upon RMR and T_b measured at 5 °C and 10 °C, the mean C_m of dormice in the present study, was 0.145 ± 0.010

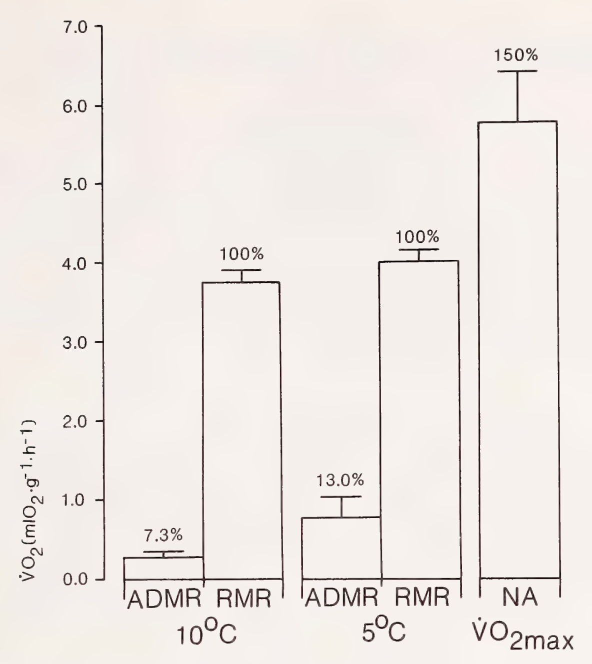


Fig. 3. The relationship between average daily metabolic rates (ADMR) during torpor and resting metabolic rate (RMR) during normothermia measured at 10 °C and 5 °C in 3 *Graphiurus murinus.* As an indication of non-shivering thermogenic ability, the metabolic response to noradrenaline injection (NA: $\dot{V}O_{2max}$) of 2 *G. murinus* is displayed to the right. Vertical lines indicate ± one standard deviation of the mean

$mlO_2 \times g^{-1} \times h^{-1} \times °C^{-1}$ with a mean normothermic T_b of 34.4 ± 0.4 °C. Using NST to produce a $\dot{V}O_{2max}$ of 5.75 $mlO_2 \times g^{-1} \times h^{-1}$ these dormice could feasibly maintain a similar T_b down to T_a's as low as −5 °C, which corresponds to the mean daily minimum temperature (−3 °C) recorded at Vaalkop Dam during winter (June/July: Pretoria Weather Bureau).

The body mass cycle displayed by *G. murinus* in the present study is similar to that reported for *Glis glis* and *E. quercinus* during winter and following cold acclimation (Mrosovsky 1986; Pajunen 1986). These dormice undergo a distinct increase in body mass prior to hibernation, during which up to 25 % of body mass is subsequently lost (Jallageas and Assenmacher 1986). In order to assess whether or not *G. murinus* displays similar body mass cycles in nature the mass of 77 specimens collected throughout the southern African subregion were grouped by month of capture and presented in the Table.

These specimens did not display a clear circannual cycle of body mass, which sugests that *G. murinus* does not naturally enter hibernation throughout southern Africa. Indeed,

Mean body mass of 77 *G. murinus* collected throughout the southern African subregion
(From the archives of the Transvaal Museum, Pretoria)

Month	Jan/Feb	Mar/Apr	May/Jun	Jul/Aug	Sep/Oct	Nov/Dec
Mass	21.6 g	22.5 g	25.0 g	23.6 g	23.7 g	22.5 g
S.D.	±8.3 g	±8.5 g	±8.5 g	±4.4 g	±5.9 g	±7.0 g
n	21	22	6	9	13	6

the cycle of body mass observed in the present study may have been an artefact of laboratory conditions as both short photoperiod (König 1960) and abundant food (Rothwell and Stock 1986) have been reported to elicit increased body mass and subsequent hibernation in other species of dormice. However, under similar conditions, Eisentraut (1962) could not elicit torpor or hibernation from *G. murinus haedulus* from tropical West Africa which suggests that different populations of this species differ in their ability to display torpor and/or hibernate. Similar geographic differences have been reported for forest dormice (*Dryomys nitedula*) which hibernate for 6 months in Eurasia yet remain active throughout the year in Israel (NEVO and Amir 1964). It therefore appears that *G. murinus* from southern Africa differ from tropical populations in their ability to enter deep torpor/hibernation, although, like garden dormice in Morocco, this ability is probably only expressed when local climatic conditions demand (Moreno and Delibes 1964).

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Zusammenfassung

Thermoregulation und Torpor bei afrikanischen Baumschläfern, Graphiurus murinus, nach Kältebelastung

Zahlreiche Arten der Gliridae aus den gemäßigten Klimazonen sind Winterschläfer. Über einen saisonbedingten Torpor bei Baumschläfern (*Graphiurus murinus*) aus den tropischen und subtropischen Gegenden Afrikas liegen nur Vermutungen vor. Drei erwachsene *G. murinus* wurden im Herbst im südlichen Afrika gefangen und im Labor 50 Tage lang bei 15 °C und 10 °C sowie unter kurzer Lichtperiode gehalten. Sie gerieten dabei in Torpor. Die Körpertemperaturen sanken bis auf den Wert der Umgebungstemperatur. Die durchschnittliche Stoffwechselintensität fiel bei 10 °C und 5 °C bis auf 7,3 % bzw. 13,0 % des Ruhewertes im normothermen Zustand. Die durch Noradrenalin induzierte zitterfreie Thermogenese übertraf die für das Erwachen aus dem Torpor benötigte Wärme. Die Bilche reagierten auf die Kältebelastung mit einer Gewichtszunahme und mit nachfolgendem Gewichtsverlust. Tiere, die im Verlaufe des Jahres gefangen wurden, zeigten diesen Zyklus nicht. Vermutlich gibt es bei *G. murinus* nur unter sehr ungünstigten klimatischen Bedingungen Torpor.

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Time budgets of Waterbuck *(Kobus ellipsiprymnus)* of different age, sex and social status

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Abstract

Daytime budgets of waterbuck *(Kobus ellipsiprymnus)* of different age, sex, and social status were measured at Lake Nakuru National Park, Kenya.

Adult and subadult females spent more time feeding than adult and subadult males. Inside territories, females spent more time feeding than outside of territories. Time spent for agonistic behaviour was highest in young males. Satellite males spent less time for sexual behaviour than territory holders, but more time than bachelor males. Territory holders and satellite males spent the same amounts of time feeding – much more than bachelor males. Because the amount of forage ingested by ruminants is positively correlated with forage quality, this indicates that bachelor males were relegated to nutritionally inferior areas. Time budgets of males and females, site preferences of females, and faecal crude protein content of animals feeding at different sites (Tomlinson 1979) all suggest that territories are high quality feeding areas and that the social system of waterbuck is a resource defence polygyny.

Sex differences in time spent feeding at the same site probably reflect a fundamental difference in the behavioural programming of males and females: females of polygynous species are more likely to be "energy maximisers" than males. Recent evidence points to differences in levels of sexual hormones as a proximate cause of sex differences not only of sexual and agonistic behaviour but also of maintenance behaviour.

Introduction

Regardless of age, sex, or social status, all members of a species have the same amount of time available to spend every day. They can, of course, be expected to spend it on different activities. In polygynous species, adult males will spend time to acquire females, whereas adult females will spend time to produce viable offspring (Schoener 1971; Trivers 1972; Clutton-Brock et al. 1982; Hoffman 1983; Owen Smith 1984). As the amount of time per day is a finite value, spending more time for one activity must mean spending less time for one or several other activities. This study shows how the age classes, sexes, and holders of different social status of a polygynous mammal differ in allotting time to their activities during the day.

Waterbuck *(Kobus ellipsiprymnus)* are antelopes similar in size to red deer; they occur throughout Africa south of the Sahara (Dorst and Dandelot 1970; Haltenorth and Diller 1977). The social structure of waterbuck living in Lake Nakuru National Park, Kenya, has been described previously (Wirtz 1981, 1982). With an average of 30 waterbuck/km^2, Lake Nakuru NP has by far the highest population density recorded for the species. Probably as a consequence of the high population density, only about 7 % of the adult males held a territory during the study period and half of the territory holders tolerated one or several additional adult males, "satellite males", in the territory. Within the territory, satellite males were subdominant to the territory holder and participated in the defence of the territory. About 9 % of the adult males acted as satellite males and the remaining 84 % were bachelor males spending most of their time outside territories. Females moved in herds of changeable size and composition over home ranges encompas-

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sing several territories and non-territorial areas. Most territories were located along the lake shore and along rivers. During the day most females were inside territories (WIRTZ 1982).

Material and methods

Study area and recording technique

The study area has been described previously (WIRTZ 1982) in a paper that also gives the definitions of the age classes used: adult male, young male, juvenile male, adult female, subadult female, and calf.

Both study years (1978 and 1979) were exceptionally wet years compared to long-term means (KUTILEK 1975); see figure 2 in WIRTZ (1982) for the monthly rainfall values. Data on time budgets were collected throughout the course of the two study years.

Time budgets of the different age classes, sexes, and social classes (territory holder, satellite male, bachelor male) were measured between 7 am to 7 pm. Groups of animals were observed with binoculars (Leitz Trinovid 10 × 40) from a Land-Rover or from tree hides. Observations were recorded on a tape recorder. The animals were accustomed to cars and during observations would graze as close as 5 m from the Landrover; average observation distance is estimated to be about 50 m. Uninterrupted observations at the same site lasted from one to twelve hours, on average three hours.

Data were collected using the „scan sampling" technique (ROLLINSON et al. 1956; ALTMAN 1974; MARTIN and BATESON 1986). The observer would scan the group at regular intervals and record the momentary activity of each animal seen. The proportion of records of a behaviour pattern is an approximation of the proportion of time spent performing this behaviour pattern. Inter-scan interval was five minutes. Large groups sometimes took longer to scan and the inter-scan interval was then set at ten minutes.

All activities were classified into the eleven types described below (see WALTHER [1958] for a description of behaviour patterns such as Flehmen, and see TOMLINSON [1980] for a description of the expressive behaviour of waterbuck in particular):

1.	Browsing	Feeding on dicotyledons, such as shrubs or *Acacia* leaves
2.	Grazing	Feeding on grasses
3.	Standing	Standing on all four legs; part of the time in this position is spent ruminating
4.	Lying head up	Lying on the ground with head raised above the ground; part of the time in this position is spent ruminating
5.	Lying head down	Lying with the head resting on the ground
6.	Walking	Moving forward at slow to moderate speed
7.	Running	Trotting or galloping
8.	Agonistic	Female butting her head into the flank of another female; male confronting another male with head raised high and horns tipped forward; male approaching another male in submissive low stretch posture with horns tilted backwards; males fighting with interlocked horns; male galloping after another male
9.	Sexual	Male sniffing female, rubbing a female with its head, performing Flehmen or Laufschlag, running after a female, attempting to mount or mounting a female, copulating
10.	Grooming	Scratching the own body with hoof or horn, licking own body (allogrooming was only observed in mothers grooming their calves; this was recorded as "others")
11.	Others	Drinking, defaecating and any other behaviour not mentioned above; also behaviour recorded as "unidentified" when an animal was partially hidden by the vegetation (0.1 % to 1.0 % of all records in the different age classes).

The observations are biased in at least the following ways. Only groups of more than five animals were used for activity records. Among other things, this means that the data for territory holders apply only to territory holders that have females with them and not to territory holders without females. Observations were made only on groups in open grassland, open shrub, and open forest but not on groups in dense shrub and dense forest where animals were difficult to see. Less than 6 % of the waterbuck were recorded in these two types of habitat during counts of habitat utilization (WIRTZ and KAISER 1988). Nevertheless, a slightly higher proportion of "browsing" would probably have been recorded if these two types of habitat had not been ignored. Recording the activity of each animal at the moment it is seen through the binoculars meant that an animal walking a few steps whilst grazing was recorded as "walking" rather than "grazing". Bouts of ruminating are frequently interrupted and animals seen at such moments were then recorded as "standing" or "lying head up" instead of "standing ruminating" or "lying ruminating". We therefore decided not to report values for the two

incomplete measures of ruminating activity and have included them in "standing" and "lying head up", respectively.

The data presented here describe daytime activity of waterbuck at Lake Nakuru National Park. Waterbuck are also active at night. For technical reasons, only few quantitative observations on nighttime activity could be taken. During several clear nights, approximately 20 hours of observations were made and there was no indication that the major patterns might be different from those recorded during daytime.

Number of observations

A total of 957643 observations were taken between 7:00 h and 19:00 h (observations per hour: 5513, 8630, 8480, 8516, 8305, 7855, 6845, 9048, 9906, 8812, 11422, 2411). The numbers of observations for the different waterbuck classes are given in Tables 1–4. The data for territorial males are from 39 individuals, those for satellite males from 36 individuals. More than 100 different individuals contributed to the observations for adult females and for bachelor males.

Treatment of data and statistical procedure

Numbes of observations were unequally distributed through the course of the day. For instance, relatively more observations were taken during hours when the animals spent most of their time grazing; a daily mean from unweighted data would then result in an overestimate of this activity. For each hour, the number of observations of each activity was expressed as the percentage of all observations during this particular hour; the daytime mean was then calculated from these percentages (cf Figure as an example).

When comparing two different waterbuck classes, their daytime means were reconverted into frequencies of observations on the basis of the total numbers of observations. The proportions of an activity in the total time budget (e.g. number of observations "grazing" versus number of observations of all other activities) were then compared by chi-square test.

When there were fewer than 100 observations for one of the classes compared during one of the hours of the day, this hour was exluded from the comparison.

Daytime budget of the "average waterbuck" was calculated by combining the data for all age classes in the proportions at which they were collected, i.e. by simply summing all observations per hour of all animals, regardless of age, sex, and social status.

The shorter the inter-scan interval, the better the estimate of the true amount of time spent for various activities (Harker et al. 1954). On the other hand, very short observations intervals can result in measuring the same phenomenon repeatedly and producing "dependent data", i.e. an inflated sample size unsuitable for statistical analysis. Scanning a group every five minutes may lead to dependent data for some activities with very long bout lengths. A statistical comparison would then lead to unrealistic levels of significance. To be on the safe side, we here call a difference "significant" only if $p < 0.001$ (chi-square value > 10.83, 1 degree of freedom).

Results

The "average waterbuck"

The "average waterbuck" spent 37 % of its daytime feeding (35.9 % grazing plus 1.1 % browsing), 15.5 % standing, 37.8 % lying, 6.7 % walking and less than 3 % for all other activities (Fig.). The two social behaviour patterns "agonistic" and "sexual" took up only 0.3 % each of the daytime activity of the "average waterbuck". Lying head down also was a comparatively rare behaviour, taking only a few minutes at a time, as is typical for large bovids (Balch 1955).

The Figure shows the distribution of the major (most time consuming) activities throughout the day. There was a morning and an evening peak of the activities grazing and walking and a corresponding midday peak of lying. Solar radiation at Nakuru reaches a maximum at about 13–14 h (Vareschi 1982, Fig. 3a), i.e. the time when the animals spent the highest proportions lying head up (48 %) and lying head down (2.4 %).

The distribution pattern of the activities throughout the course of a day as shown in the Figure was essentially the same for all classes of waterbuck. In the following, we therefore compare only the daily means of animals of different age, sex, and social status.

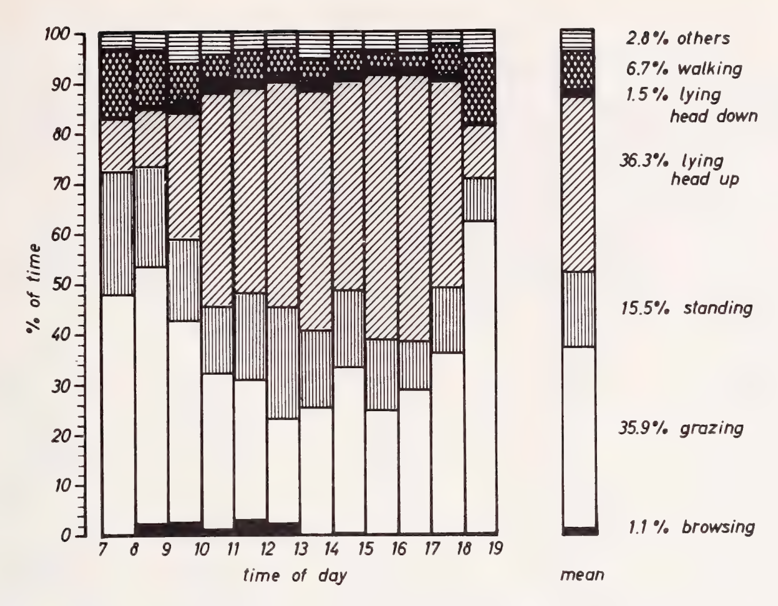


Fig. 1. Distribution of activities of the "average waterbuck" through the course of a day and daily means of the different activities. See text for numbers of observations per hour

Sex differences

Adult male – adult female

Adult males and adult females differed markedly in their time budgets (Table 1). Whereas adult males spent 26.8 percent of their time feeding, adult females spent 39.7 percent – almost 1.5 times as long as males (chi-square 877, $p < 0.00001$). In contrast, adult males spent more time lying than adult females (chi-square 464, $p < 0.00001$). Note that the majority of these adult males are bachelor males and that the time budget of adult males in general is therefore largely determined by the time budget of bachelor males. A comparison of the time budgets of bachelor males, territory holders, and satellite males is given below.

Table 1. **Comparison of time budgets (% of observations) of adult males, adult females, and subadult females (7–19 h)**

	Adult male	Adult female	Subadult female
Browsing	0.4	1.3	1.2
Graszing	26.4	38.4	38.1
Standing	15.1	15.3	15.4
Lying head up	43.0	34.5	31.7
Lying head down	2.2	1.1	1.2
Walking	5.6	6.6	8.0
Running	0.2	0.2	0.2
Agonistic	0.5	0	0.2
Sexual	2.1	0	0
Grooming	4.1	2.3	3.8
Others	0.4	0.3	0.2
n observations	18 844	32 958	14 821

Juvenile male – subadult female

For juvenile males, we have insufficient data for the time 18 to 19 h. A direct comparison with subadult females is therefore impossible. After truncating the data for subadult females at 18 h, a comparison of juvenile males and subadult females (Table 2) also shows a

Table 2. **Comparison of time budgets (% of observations) of subadult females, juvenile males, young males, and adult males (7–18 h)**

	Subadult female	Juvenile male	Young male	Adult male
Browsing	1.3	0.5	0.6	0.5
Grazing	35.7	27.8	26.3	24.2
Standing	16.1	24.2	20.4	15.5
Lying head up	34.2	29.4	36.7	45.4
Lying head down	1.2	2.9	1.8	2.3
Walking	7.1	8.9	6.3	5.4
Running	0.2	0.3	0.2	0.1
Agonistic	0.1	0.4	1.1	0.5
Sexual	0	0	0.2	1.8
Grooming	3.9	5.3	6.2	4.0
Others	0.2	0.3	0.5	0.3
n observations	14 641	3331	12 708	18 282

large difference in the time spent feeding: whereas juvenile males spent 28.3 % of their time feeding, subadult females spent 37 % (chi-square 89.6, $p < 0.00001$). In contrast, juvenile males spent more time standing than did subadult females (chi-square 122, $p < 0.00001$).

Age differences

Adult female – subadult female

Adult females and subadult females closely resembled each other in the times spent for the different activities (Table 1). There were no obvious age differences in their time budgets. Those activities restricted to sexually mature females (e.g. suckling a calf or licking a calf) were recorded in the category "others" and took up less than one percent of the adult females' time.

Adult male – young male – juvenile male

Young males spent less time lying (38.5 %) than adult males (47.7 %) (Table 2, chi-square 262, $p < 0.00001$). Instead, they stood longer, groomed longer and spent more time in agonistic interactions (chi-square > 36, $p < 0.00001$ in each case). Feeding time of young males (26.9 %) was slightly higher than that of adult males (24.7 %) (chi-square 19.1, $p < 0.0001$).

Juvenile males spent even less time lying (32.3 %) and more time standing than young males (chi-square > 22, $p < 0.00001$ in both cases). They also spent slightly more time feeding than young males, but this difference does not reach the significance level. Juvenile males spent approximately the same amount of time for agonistic behaviour as did adult males (chi-square 0.6), i.e. much less than young males (chi-square 14.1, $p < 0.0002$).

Thus, with increasing age, males tended to spend less time standing and feeding and more time lying; time spent for agonistic interactions was highest for young males.

Social status

Territory holder – Satellite male – Bachelor male

Table 3 compares the time budgets of territory holders, satellite males and bachelor males. As there were insufficient data for bachelor males from 7 to 8 h and from 18 to 19 h, the data for the other two classes were also reduced to the time span 8 to 18 h.

Table 3. **Comparison of time budgets (% of observations) of territory holders, satellite males, bachelor males, and adult females (8–18 h)**

	Territory holder	Satellite	Bachelor	Adult female inside territory
Browsing	0.4	1.4	0.4	1.3
Grazing	28.1	27.2	19.3	37.3
Standing	14.4	18.1	13.1	14.3
Lying head up	39.9	36.7	49.1	38.5
Lying head down	2.0	1.3	2.6	1.3
Walking	6.5	5.7	4.3	4.4
Running	0.2	0.2	0	0.1
Agonistic	0.7	0.4	0.8	0
Sexual	5.1	3.0	0.5	0
Grooming	2.1	5.6	9.3	2.4
Others	0.6	0.4	0.6	0.4
n observations	2886	2215	11 828	21 808

Territory holders and satellite males spent the same amounts of time feeding (28.5 % and 28.6 %); in contrast, bachelor males spent much less of their time feeding (19.7 %; chi-square > 88, $p < 0.00001$ for both comparisons).

Bachelor males spent more than half (51.7 %) of their daytime hours lying head up or head down. Satellite males and territory holders spent much less time for this type of activity (38 % and 41.9 %; chi-square > 89, $p < 0.00001$ in both cases). Compared to territory holders, satellite males stood longer (chi-square 12.4, $p < 0.0004$) but spent less time lying; however, the latter difference does not reach the predetermined significance level (chi-square 7.7, $p < 0.005$).

Bachelor males spent more time grooming themselves than did satellite males (chi-square 32, $p < 0.00001$), which in turn spent more time grooming themselves than did territory holders (chi-square 43.5, $p < 0.00001$).

Whereas territory holders spent 5.1 % of their time for sexual behaviour, bachelor males spent only a tenth of this time on sexual behaviour (chi-square 354.8, $p < 0.00001$). Satellite males spent less time on sexual behaviour than territory holders, but spent considerably more time on sexual behaviour than did bachelor males (chi-square 13.9, $p < 0.0002$ for comparison with territory holders, chi-square 130.1, $p < 0.00001$ for comparison with bachelor males).

Territory holders with and without Satellite males

Table 4 compares the time budgets of territory holders when a satellite male was present and of territory holders in the absence of a satellite male. Because of insufficient data for the time period of 18 to 19 h in one of the classes, both data sets are truncated at 18 h. Territory holders without satellite males spent more time grazing, less time lying and more time for sexual activities but none of these differences reached the predetermined level of significance (6.95 > chi-square > 6.30, $0.02 > p > 0.005$).

Table 4. **Comparison of time budgets (% of observations) of territory holders with satellites and territory holders without satellites and of adult females inside territories and adult females outside territories**

	Territory holder with satellite (7–18 h)	Territory holder without satellite (7–18 h)	Adult female inside territory (8–12, 14–16, 17–18 h)	Adult female outside territory (8–12, 14–16, 17–18 h)
Browsing	0.6	0.2	1.4	2.6
Grazing	23.5	27.2	41.1	27.6
Standing	14.2	14.5	13.9	15.8
Lying head up	41.9	37.6	34.4	36.0
Lying head down	2.2	2.0	1.3	1.9
Walking	6.6	5.4	4.9	2.9
Running	0.2	0.2	0.1	1.0
Agonistic	0.6	0.8	0	0
Sexual	6.6	9.2	0	0
Grooming	3.2	2.0	2.5	10.9
Others	0.4	0.4	0.4	1.3
n observations	1548	1548	15 217	1644

Adult females inside territories and outside territories

During the day, most females were inside territories. Even though adult females were the largest class in the population (31 % of the waterbuck seen during monthly road strip counts were adult females, Wirtz and Kaiser 1988), there were insufficient data for the time budgets of adult females outside territories for five of the twelve daytime hours. A comparison between adult females inside territories and adult females outside territories (Table 4) can therefore only be made for the following fragments of a day: 8–12, 14–16, and 17–18 h.

When inside territories, adult females spent much more time grazing (41.1 %) than when outside territories (27.6 %) chi-square = 112, $p < 0.00001$). Outside the territories, adult females spent more time browsing (chi-square = 13.8, $p < 0.0002$) and grooming themselves (chi-square 323, $p < 0.00001$) than inside territories.

Sex differences revisited : adult females – adult males, inside territories

The time budgets of adult females and of adult males were compared in a previous section. However, the two data sets differ not only in the sex of the animals but also in the location where they were taken: the majority of the data for adult males are of bachelor males (i.e. from outside territories), and the majority of the data for adult females are from females inside territories. To eliminate the bias caused by differences in site of observation, the time budget of adult females inside territories has to be compared with that of adult males inside territories. Table 3 shows the time budget of adult females (between 8 and 18 h) in comparison with that of territory holders and satellites.

Inside territories, females still spent much more time feeding than did males (chi-square > 85 in both comparisons, $p < 0.00001$). The sex difference in time spent lying, however, is no longer significant when considering only animals inside territories (chi-square 4.6 in the comparison with territory holders, $p < 0.05$; chi-square 2.6 in the comparison with satellite males, $p < 0.15$). Adult females outside territories and inside territories differed conspicuously from adult males in spending almost no time on agonistic and sexual interactions ($p < 0.00001$ for all comparisons).

Discussion

An understanding of the nutritional physiology of ruminants is essential for the interpretation of their time budgets. The food intake of ruminants is limited by the time required to process the food in the rumen. They can ingest food only as fast as they can digest it. Better digestible forage moves faster through the digestive system and thus permits the animal to take up more of it. Low digestibility of food cannot be compensated for by a greater food intake – on the contrary, food intake is reduced because the time required for processing is longer. Except for highly digestible food (Ammann et al. 1973), the amount of forage ingested and the time spent feeding are positively correlated with the quality of the forage (Blaxter 1962; Thornton and Minson 1972; Arnold 1985). Waterbuck are "grass and roughage eaters" taking food of comparatively low digestibility requiring relatively long processing times (Hofmann 1973).

The social structure of Lake Nakuru waterbuck

Inside territories, females spent more time feeding than outside territories. This indicates better quality of the forage conditions inside territories. Females are free to move between these areas and the observation that female density is higher inside than outside territories (Wirtz 1982) suggests that territories are superior feeding sites. However, there could also be alternative and additional reasons for the female preference for territories (e.g. more frequent harassment by bachelor males outside territories). Adult males show similar site differences in feeding times: bachelor males spent less time feeding than territory holders and their satellite males. Waterbuck territories usually border on water and, to the human observer, the grass outside territories often appeared to be higher and dryer. Dry grass usually has a higher proportion of lignin and thus a lower digestibility (cf Sinclair 1975), which would cause longer processing times and lower rates of uptake.

Protein content is generally acknowledged as a major determinant of nutritive value of forage for ruminants (Sinclair 1975; Festa-Bianchet 1988 and references therein). Faecal crude protein content is closely correlated with dietary protein and has been used to assess forage quality in studies of domestic cattle (Bredon et al. 1963) and wild ungulates (see references in Festa-Bianchet 1988). In a Rhodesian population of waterbuck, the faeces of territory holders and of adult females had a higher crude protein content than the faeces of bachelor males (Tomlinson 1979). This Rhodesian population of waterbuck had the same social structure as Nakuru waterbuck suggesting that Tomlinson's (1979) results would also apply to Nakuru waterbuck. Site-dependent differences in faecal crude protein of males, site preference of females, site-dependent foraging times of females, and site-dependent foraging times of males all suggest that territories are high quality feeding areas. Bachelor males, being excluded from territories, are probably relegated to inferior feeding areas.

The spatial distribution of resources determines the distribution of receptive females, which in turn determines the distribution of males and hence the nature of the mating system (see Emlen and Oring 1977 for a general discussion and classification of social systems, and Geist 1974 for the relationship of ecology and social evolution of ungulates in particular). Territory holders defend high quality feeding sites preferred by females and mate with the females coming to these areas. In the terminology of Emlen and Oring (1977), the mating system of waterbuck is a "resource defence polygyny". (Unfortunately, in their influential paper on the evolution of mating systems, Emlen and Oring [1977], erroneously refer to waterbuck as an example of "female defence polygyny".)

In contrast to females (see below), the fitness of males of a polygynous species, such as waterbuck, is probably determined by non-foraging activities, in particular efforts to acquire females. Because comparatively little time is spent in aggressive encounters, the sex

difference in aggressive behaviour, likely to be very important in terms of energy and mortality risk, is only weakly expressed in the time budgets. Territory ownership did not cause a reduction in feeding time. On the contrary, territory owners spent more time feeding, on more nutritious food, than did bachelor males. The costs of territoriality are only weekly expressed in the time budgets by slightly higher percentages of walking and running. The differences in energy budget and risk are probably more important.

Sex differences

Even when feeding at the same site and presumably on forage of the same nutritional value, females spent much more time on energy intake than males – a difference already apparent in subadult animals. With increasing age of males (from juvenile male via young male to adult male), this sex difference in maintenance behaviour became more and more pronounced. Spinage (1968) observed the activity of three individually known adult female waterbuck and two individually known adult males (one of them a territory holder) in the Queen Elizabeth Park, Uganda, for continuous periods of up to three consecutive days. The absolute values of his data are not directly comparable with those of the present study, because an animal walking a few steps from one grazing site to another was recorded as "walking" at Nakuru but recorded as "grazing" by Spinage. Nevertheless, Spinage's data similarly show sex-specific differences in maintenance behaviour: the three females spent more time feeding than the two males.

Female waterbuck are probably "energy maximisers" in the terminology of Schoener (1971), i.e. their fitness is determined mainly by the amount of energy acquired. That females spend more time feeding than males is a general finding for all ungulates studied (cf review by Bunnell and Gillingham 1985) and also for several other animal species (e.g. Hoffman 1983). This difference is probably a fundamental behavioural and physiological difference between the sexes, rather than an epiphenomenon of other factors such as differences in bite size. Jewell (1986) showed that in a feral population of sheep at St. Kilda Island, Scotland, rams spent much less time grazing than ewes. Interestingly, castrated males spent almost as much time grazing (71 %) as females. The likely basis for these differences lies in low testosterone levels of castrated males and the accompanying shift to a female type of maintenance behaviour. The proximate cause for the sex difference not only in aggressive and sexual behaviour but also in maintenance behaviour of ruminants could thus be a difference in levels of sexual hormones.

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Zusammenfassung

Zeitbudgets bei Wasserböcken (Kobus ellipsiprymnus) von unterschiedlichem Alter, Geschlecht und Sozialstatus

Im Nakuru Nationalpark, Kenia, wurde gemessen, wie sich Wasserböcke von unterschiedlichem Alter, Geschlecht und Sozialstatus die Tageszeit einteilten. Weibchen verbrachten mehr Zeit mit Fressen als Männchen und innerhalb von Territorien mehr als außerhalb. Bei jungen Männchen war der Anteil Zeit für kämpferische Interaktionen am höchsten. Satellitenmännchen verbrachten zwar weniger Zeit mit sexuellen Aktivitäten als Territoriumsbesitzer, aber mehr als Junggesellenmännchen. Territoriumsbesitzer und Satellitenmännchen wendeten gleich viel Zeit für Fressen auf – wesentlich mehr als Junggesellenmännchen. Da bei Widerkäuern Nahrungsqualität und Nahrungsaufnahme negativ korrelieren, deutet dies an, daß die Junggesellenmännchen in Gebiete schlechterer Futterquali-

tät abgedrängt wurden. Sowohl die Zeitbudgets von Männchen und Weibchen, als auch die Ortsbevorzugung der fressenden Weibchen und der Proteingehalt von Kotproben (TOMLINSON 1979) deuten an, daß Wasserbock-Territorien Orte hoher Futterqualität sind, und daß das Sozialsystem von Wasserböcken als Fortpflanzungsterritorialität bezeichnet werden kann.

Geschlechtsunterschiede im Zeitaufwand für Nahrungserwerb reflektieren wahrscheinlich fundamentale Unterschiede im Verhaltensprogramm von Männchen und Weibchen: bei polygynen Arten sind Weibchen wahrscheinlicher "Energiemaximierer" als Männchen. Neuere Untersuchungen deuten an, daß unterschiedliche Niveaus von Sexualhormonen der proximale Grund nicht nur von Geschlechtsunterschieden im Sexualverhalten und im kämpferischen Verhalten sind, sondern auch der proximale Grund von Geschlechtsunterschieden im Ernährungsverhalten.

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Some remarks on size differences of northwest German game populations from Neolithic to modern times

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Starting-point of this consideration is the bone material from medieval Schleswig, excavation Schild (Vogel 1983). For a certain period during the Middle Ages Schleswig, situated in the northern part of Schleswig-Holstein (Fig. 1), was one of the most important trade centres in Europe, i.e., from the 11th century after the decline of nearby Haithabu until the middle of the 13th century when Lübeck, situated 100 km southeastwards and finally the capital of the Hanseatic League, succeeded in its place (Hoffmann 1981).

At the excavation site nearly 112 000 bones of mammals were found. Only 1 350 of these bones, which is a small fraction of 1.2 %, were from wild mammals, the rest from domestic ones (Hüster 1990). This is typical for medieval sites (Reichstein et al. 1980). According to the relative frequencies of the remains the most important game were the artiodactyl species red deer (n = 397), roe deer (n = 323) and wild boar (n = 82), and further the brown hare (n = 312) and red fox (n = 97). Although the amount of bone material of



Fig. 1. Schleswig-Holstein. Location of the medieval trade centres Haithabu, Schleswig, and Lübeck as well as some other medieval settlements

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these species is hardly satisfactory, it was the basis for size analyses, and was compared with corresponding bones not only from other early historic and prehistoric sites, but also with recent skeletal material (collection of Institut für Haustierkunde, University of Kiel).

In roe deer and in wild boar no size differences are apparent between the Schleswig material and that of other medieval or neolithic sites. However, compared with recent skeletons from Schleswig-Holstein it is obvious that roe deer and wild boar today are significantly smaller than the individuals of these species identified for medieval Schleswig and for the other sites. In roe deer this is shown by the measurements 'maximum length' of radius and metacarpus and 'distal width' of metacarpus (Fig. 2).

This tendency – evident differences in size between pre- or early historic findings and recent skeletal material – is also true for red deer (Fig. 3). In any case the recent material is relatively small-sized and corresponding differences in body size can be deduced. But the comparison of the Schleswig material with other subfossil bones has shown that red deer of the early medieval strongholds Scharstorf and Bischofswarder, situated in eastern Holstein, partly must have been even larger. This is shown by the measurement 'maximum length' of calcaneus, whereas similar differences cannot be established in phalanx 1, the second skeletal element analysed.

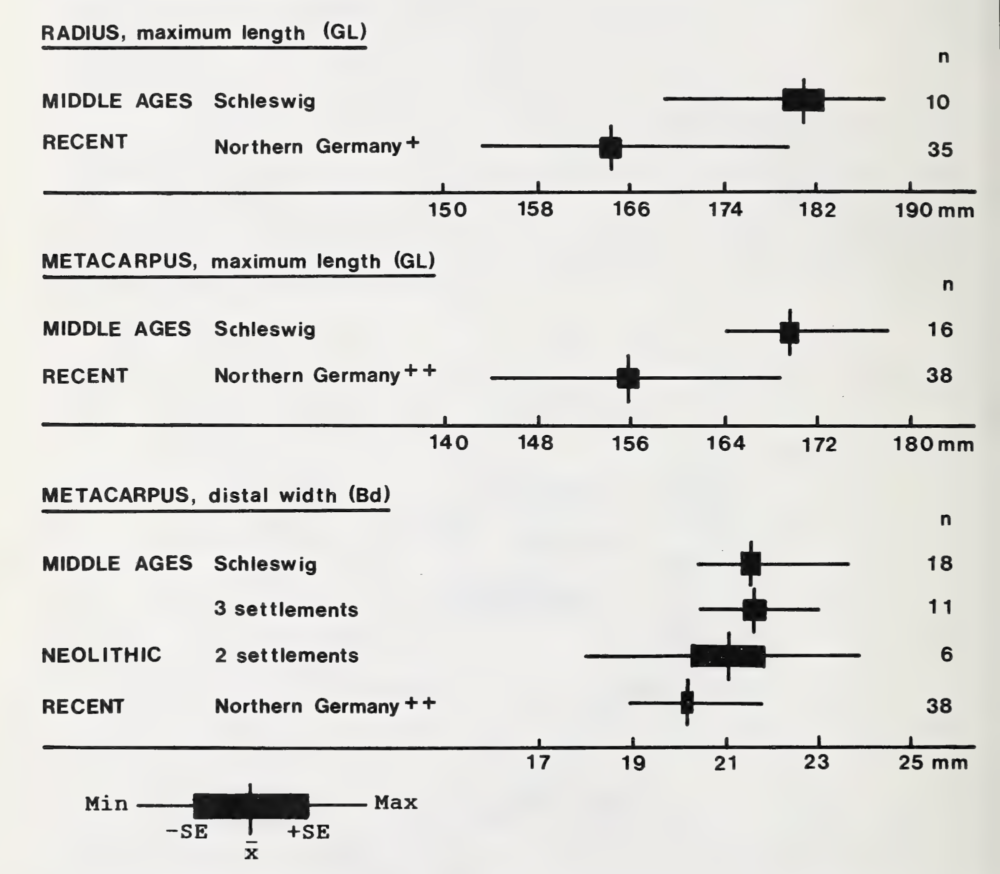


Fig. 2. Roe deer, *Capreolus capreolus.* Comparison of size between finds from Schleswig, various northwest German sites (Middle Ages: Haithabu – Reichstein 1990; Lübeck Königstraße – Paul 1980; Hitzacker – Walcher 1978; Neolithic: Hüde I – Hübner et al. 1988; Rosenhof – Nobis 1975) and recent material; + 24 ♀♀, 11 ♂♂; ++ 25 ♀♀, 13 ♂♂

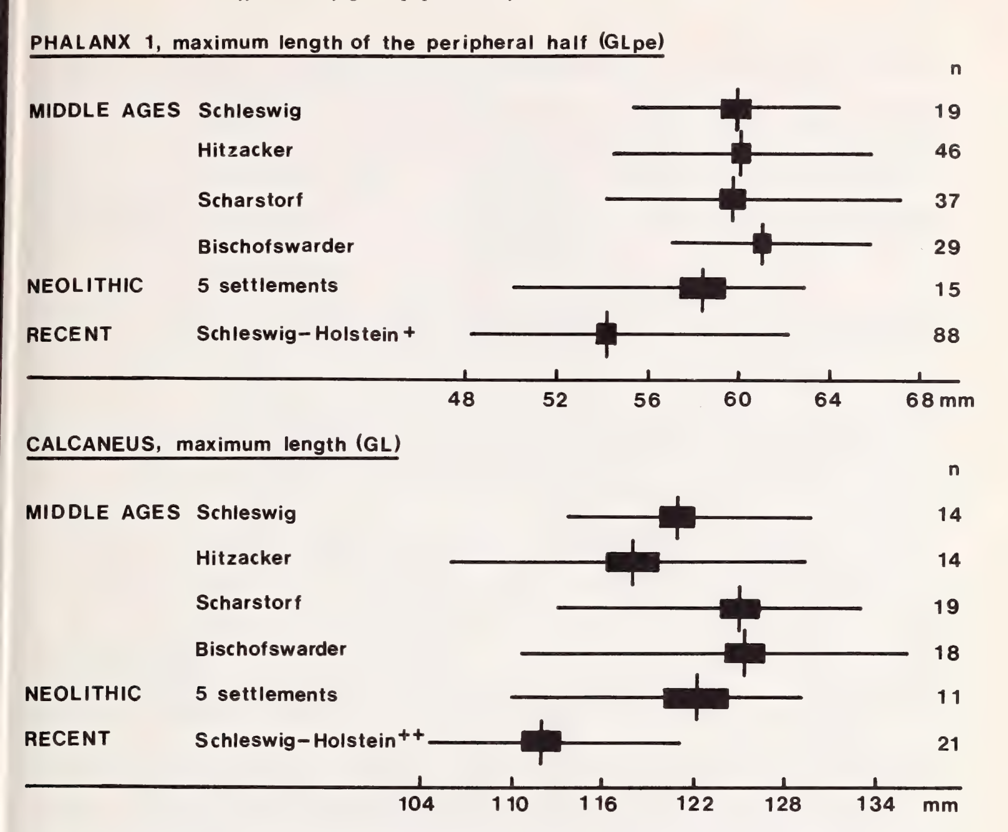


Fig. 3. Red deer, *Cervus elaphus.* Comparison of size between finds from Schleswig, various northwest German sites (Hitzacker – WALCHER 1978; Scharstorf – HEINRICH 1985; Bischofswarder – REICHSTEIN et al. 1980; Neolithic: Hüde I – HÜBNER et al. 1988; Bistoft – JOHANSSON 1979; Süssau – NOBIS 1971; Rosenhof – NOBIS 1975, Stinthorst – GEHL 1976) and recent material; + 7 ♀♀, 4 ♂♂; ++ 6 ♀♀, 4 ♂♂, 1 sex?

Corresponding analyses of brown hare and red fox did not yield such results. In the case of hare only very few measurements showed significant size differences, but always without a clear tendency. In the case of the fox size differences were found only in the mandibula, which is larger in recent specimens compared with those from Schleswig. In the analysis of the large amount of material of red fox from Haithabu REICHSTEIN (1990) obtained similar results.

The clear dissimilarities that could be shown especially in red deer, roe deer and wild boar, concern only size but apparently not shape. Shape differences between single bones would point to dissimilarities of the stature of animals. But when correlating two measurements of phalanx 1 anterior of the red deer by regression methods these bones of all populations converged to one straight line, which describes the allometrical relationship of the two measurements taken (RÖHRS 1959). Looking at roe deer, however, no correlations at all could be found. This points to a large variability in this species. Such methods could not be employed in the analysis of wild boar, because the quality of the material was too poor.

This size reduction in the artiodactyl species must be a modern phenomenon for one cannot see similar differences between the samples of the various early historic or prehistoric sites. This means that from neolithic to medieval times there were no changes

which could bring about diminution or enlargement. Thus, it can be noted that the degree of climatic influences in the course of this long period was too low to alter the size of the species in the sense of Bergmann's rule (climate-size-rule). Corresponding results especially for red deer and roe deer have been repeatedly shown, for instance by Boessneck (1956), Requate (1956), Reichstein (1974), and Kratochvíl (1988).

This phenomenon – no alterations in size over a long period followed by a sudden diminution in the recent past – can be explained by human influence on landscape and vegetation. Although man has modified the landscape by agricultural activities since centuries – e.g. especially the medieval clearing of woodland for cultivation – the alterations caused by human activities are becoming more extensive and frequent especially in the last few decades. Here, one must not only see the modern cultivation, but also the development of settlements and the progress of traffic. Further, one must note that modern forestry is not suitable for game. The same is true for modern hunting with its demand for trophies. Whereas these factors are essentially responsible for the diminution in red deer and probably also in wild boar, the relatively small size of roe deer, however, presumably is only indirectly connected with them: According to Klein and Strandgaard (1972) in this species size is correlated with population density to a high degree, which in return is dependent on landscape and vegetation, cover, food value etc. The above-mentioned variability of roe deer in shape must also be seen in this context (Sägesser 1966). All in all the transformation of the natural landscape to a cultural one with all of its implications can be considered the main cause for diminution of these species, which are vegetarian or partly so (*Sus scrofa*) and which are more or less confined to the woods. It cannot be decided, whether this recent size reduction is a result of mutations or – until now – only expression of a modification caused by the bad conditions of life for these species. However, it is obvious that a phylogenetic tendency of diminution like that supposed by von Lehmann (1960) in the case of roe deer after considering a far longer period cannot be the explanation for the present results, as the described size reduction is a modern event.

Hare and fox are not affected in this way. These species require quite different living conditions. Originally the hare is a mammal of the steppe. Thus, the development of the cultural landscape with fields and pastures instead of woodland improved its ecological basis, although some other living conditions were worsened. Therefore it is understandable that one cannot observe a clear trend of diminution. But one should also bear in mind, for instance, that the recent population from Schleswig-Holstein is not a truly autochthonous one: In the beginning of this century hares from many areas, especially from southeast Europe, were released here (Mohr 1931). The fox is a carnivore and for this reason is only indirectly dependent on vegetation or landscape like the other animals. Moreover it has a good ecological adaptability.

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BEKANNTMACHUNG

Einladung

Die 65. Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde e. V. findet von Sonntag, den 22. September, bis Donnerstag, den 26. September 1991, in Hamburg im Zoologischen Institut und Zoologischen Museum statt.

Vorläufiges Programm

Sonntag, 22. September:	Anreise	
	17.00 Uhr:	Vorstandssitzung
	19.00 Uhr:	Zwangloser Begrüßungsabend im Hotel Baseler Hof in der Esplanade
Montag, 23. September:	9.00 Uhr:	Grußworte und Eröffnung der Tagung durch den 1. Vorsitzenden im Hörsaal des Zoologischen Instituts und Zoologischen Museums
	9.30 Uhr:	Hauptvorträge und Vorträge zum Themenschwerpunkt „Systematik und Stammesgeschichte der Säuger"
	14.30 Uhr:	Vorträge
	17.00 Uhr:	Mitgliederversammlung
Dienstag, 24. September:	9.00 Uhr:	Hauptvortrag und Vorträge zum Themenschwerpunkt „Anpassung an aquatische Lebensräume"
	11.00 Uhr:	Posterdemonstration
	14.30 Uhr:	Vorträge
	16.30 Uhr:	Posterdemonstration
	20.00 Uhr:	Filmabend
Mittwoch, 25. September:	9.00 Uhr:	Hauptvortrag und Vorträge zum Themenschwerpunkt „Domestikation"
	14.00 Uhr:	Vorträge
	16.00 Uhr:	Führung durch Hagenbecks Tierpark
	19.00 Uhr:	Geselliger Abend im Restaurant des Tierparks Hagenbeck
Donnerstag, 26. September:		Exkursion in das östliche Schleswig-Holstein (Naturpark Lauenburger Seen)

Alle Interessenten sind herzlich eingeladen. Neben den angekündigten Themenschwerpunkten werden auch dieses Mal andere Fachrichtungen mit Vorträgen und Posterdemonstrationen berücksichtigt. Das Programm mit der Vortragsabfolge wird allen Mitgliedern – auf Anfrage auch Nichtmitgliedern – rechtzeitig vor der Tagung zugesandt. Falls persönliche Einladungen gewünscht werden, erbitten Sie diese vom 1. Vorsitzenden, Prof. Dr. E. Kulzer, Institut für Biologie III, Auf der Morgenstelle 28, W-7400 Tübingen.

Bitte melden Sie Vorträge, die nicht länger als 15 min dauern sollen, sowie Posterdemonstrationen beim Geschäftsführer unserer Gesellschaft, Prof. Dr. U. Schmidt, Zoologisches Institut, Poppelsdorfer Schloß, W-5300 Bonn 1, Tel. (02 28) 73 54 68, möglichst frühzeitig, jedoch spätestens bis zum 30. April 1991 (Ausschlußfrist) an.

Falls Sie Fragen zum Tagungsort und zur Organisation haben, wenden Sie sich bitte an Prof. Dr. H. Schliemann, Zoologisches Institut und Zoologisches Museum, Martin-Luther-King-Platz 3, W-2000 Hamburg 13, Tel. (0 40) 41 23 39 17.

Subscription information for USA, Canada and Mexiko obtainable from Paul Parey Scientific Publishers/IR Unltd., 35 West 38th Street, Suite 3 W, New York, NY 10018, USA.

Erscheinungsweise und Bezugspreis 1991: 6 Hefte bilden einen Band. Jahresabonnement Inland: 338,– DM zuzüglich 13,80 DM Versandkosten, Gesamtpreis 351,80 DM einschließlich 7% Mehrwertsteuer. Jahresabonnement Ausland: 338,– DM zuzüglich 18,– DM Versandkosten. Das Abonnement wird zum Jahresanfang berechnet und zur Zahlung fällig. Es verlängert sich stillschweigend, wenn nicht spätestens am 15. November eine Abbestellung im Verlag vorliegt. Die Zeitschrift kann bei jeder Buchhandlung oder bei der Verlagsbuchhandlung Paul Parey, Spitalerstraße 12, W-2000 Hamburg 1, Bundesrepublik Deutschland, bestellt werden. Die Mitglieder der „Deutschen Gesellschaft für Säugetierkunde" erhalten die Zeitschrift unberechnet im Rahmen des Mitgliedsbeitrages.

Z. Säugetierkunde 56 (1991) 1, 1–64

Mit einer Beilage des Verlages Paul Parey

Edgar Schallenberger

Charakterisierung von Sekretionsrhythmen der Gonadotropine und Ovarsteroide während des Brunstzyklus, der Gravidität und post partum beim Rind

(Advances in Veterinary Medicine – Fortschritte der Veterinärmedizin, No. 40)

Von Dr. Dr. E. Schallenberger, München. 1990. 117 Seiten mit 60 Abbildungen und 21 Tabellen. 25×17 cm. Kartoniert DM 68,– ISBN 3-489-51316-9

Ein aktuelles Arbeitsgebiet von Biotechnik und Medizin ist die willkürliche Steuerung und Manipulation von Fortpflanzungsfunktionen. Obwohl bei den landwirtschaftlichen Nutztieren häufig und oft durchaus erfolgreich Fortpflanzungssteuerung durchgeführt wird, sind die endokrinen Abläufe, in die eingegriffen wird, teilweise erst in Ansätzen bekannt. Deshalb werden in dieser Arbeit einige Zusammenhänge von Hormonsekretionsrhythmen beim gesunden adulten Rind während Brunstzyklus, Gravidität und Post-Partum-Phase aufgezeigt, um einen Einblick in wesentliche Grundprinzipien hierarchisch gegliederter neuroendokriner Regelsysteme zu geben. Viele der exemplarisch beim Rind aufgezeigten Zusammenhänge können zur vergleichenden Interpretation von Befunden bei anderen Spezies herangezogen werden. Die Daten sind für Veterinärmediziner, Tierproduzenten, Biologen und Endokrinologen gleichermaßen von Interesse.

Aus dem Inhalt:

Allgemeiner Überblick über die Steuerung der Reproduktion beim weiblichen Rind – Das Hypothalamus-Hypophysensystem – Endokrine Signalübertragung – Entwicklung von Versuchstechniken und Meßverfahren zur Erfassung diskontinuierlicher Hormonsekretion – Brunst- und Zyklusfeststellungen – Probenentnahmen und -konservierung – Darstellung diskontinuierlicher Hormonsekretion – Radioimmunologische Hormonbestimmung – Eigene Ergebnisse – Sekretionsmuster von Gonadotropinen und Ovarsteroiden während des physiologischen Brunstzyklus – Messungen der Gonadotropine in der V. jugularis bei 5 Minuten Probenintervall – Vergleichende Messungen in der V. cava caudalis und der V. jugularis während der Lutealphase – Vergleichende Messungen in der V. cava caudalis und der V. jugularis während der Vorbrunst- und Brunstphase – Hormonsekretionsmuster während der Gravidität – Diskussion der eigenen Befunde – Hypophysen- und Gelbkörperfunktion p. p. – Regelkreis wichtiger Fortpflanzungshormone – Allgemeine Schlußfolgerung bezüglich der Relevanz der untersuchten Hormone in Blutproben – Summary.

Berlin und Hamburg

PAUL PAREY

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Die Zeitschrift für Säugetierkunde veröffentlicht Originalarbeiten und wissenschaftliche Kurzmitteilungen aus dem Gesamtgebiet der Säugetierkunde, Besprechungen der wichtigsten internationalen Literatur sowie die Bekanntmachungen der Deutschen Gesellschaft für Säugetierkunde. Verantwortlicher Schriftleiter im Sinne des Hamburgischen Pressegesetzes ist Prof. Dr. Dieter Kruska.

Zusätzlich erscheint einmal im Jahr ein Heft mit den Abstracts der Vorträge, die auf der jeweiligen Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde gehalten werden. Sie werden als Supplement dem betreffenden Jahrgang der Zeitschrift zugeordnet. Verantwortlich für ihren Inhalt sind ausschließlich die Autoren der Abstracts.

Manuskripte: Manuskriptsendungen sind zu richten an die Schriftleitung, z. Hd. Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Biologie-Zentrum, Neue Universität, Olshausenstr. 40–60, W-2300 Kiel, Bundesrepublik Deutschland. Für die Publikation vorgesehene Manuskripte sollen gemäß den „Redaktionellen Richtlinien" abgefaßt werden. In ihnen finden sich weitere Hinweise zur Annahme von Manuskripten, Bedingungen für die Veröffentlichung und die Drucklegung, ferner Richtlinien für die Abfassung eines Abstracts und eine Korrekturzeichentabelle. Die Richtlinien sind auf Anfrage bei der Schriftleitung und dem Verlag erhältlich.

Sonderdrucke: Anstelle einer Unkostenvergütung erhalten die Verfasser von Originalbeiträgen und Wissenschaftlichen Kurzmitteilungen 50 unberechnete Sonderdrucke. Mehrbedarf steht gegen Berechnung zur Verfügung, jedoch muß die Bestellung spätestens mit der Rücksendung der Korrekturfahnen erfolgen.

Fortsetzung 3. Umschlagseite

Z. Säugetierkunde 56 (1991) 65–71

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Comparative gut morphometrics of Vervet *(Cercopithecus aethiops)* and Samango *(C. mitis erythrarchus)* monkeys

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Abstract

A comparative morphometric examination of the gastrointestinal tracts of vervet *(Cercopithecus aethiops* and samango *C. mitis erythrarchus* monkeys revealed that samangos possess significantly larger volumes in the hindgut (caecum and colon). The surface area of the main absorptive region of the gastrointestinal tract (the small intestine) was also larger in samangos than in vervets. Samangos include larger amounts of fibrous leaf material in their diets than vervets, and the importance of the larger volumes are discussed with reference to the fermentative process required to digest and utilise this foliar component.

Introduction

The structure of the gastrointestinal tract (GIT) is fairly homogeneous among different orders of mammals (Chivers and Hladik 1980), and development of different parts of the GIT generally reflect adaptations to different foods. Plant food with a high content of structural carbohydrates can be digested with the help of microbes in either the stomach or the hindgut, where the enzymes produced by the microbes degrade the food and render its chemical constitutents absorbable (Langer 1988). Among the African primates are examples of both foregut (stomach) and hindgut (caecum and colon) fermenters. The folivorous colobines possess plurilocular, haustrated stomachs, while most of the frugivorous/omnivorous cercopithecines possess simple unilocular, glandular stomachs (Langer 1988), a well-developed caecum and a large and haustrated colon.

The gross morphology and ultrastructure of the GIT of vervet monkeys *(Cercopithecus aethiops)* and samango monkeys *(C. mitis)* is similar (Bruorton 1989). Samangos are frugivorous, but include a relatively high proportion of leaves in their diets (Rudran 1978; Cords 1987; Lawes 1990), while vervets are generally regarded as frugivorous/omnivorous and consume roughly equal proportions of fruit and animal (mostly insect) material (Dunbar and Dunbar 1974; Kavanagh 1978; Watson 1985). GIT morphology may show considerable variation even between frugivorous primate species, depending on the amount of insects or leaves included in the primarily fruit diet (Chivers and Hladik 1980), and this may include expansion within the tract. This is usually associated with the fermentation process, since the larger the volume, the more fermentation can occur (Chivers and Hladik 1980).

A comparative examination was initiated to determine whether the volumes of various regions of the gastrointestinal tract (and surface area of small intestine) differ significantly between the two primate species. Volumes are indicators of physiological processes, such as microbial digestion, that are important in herbivore nutrition. This comparative examination might therefore assist in providing an explanation of the digestive strategies of the two species, and in determining how samangos digest the foliar components of their diet.

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Materials and methods

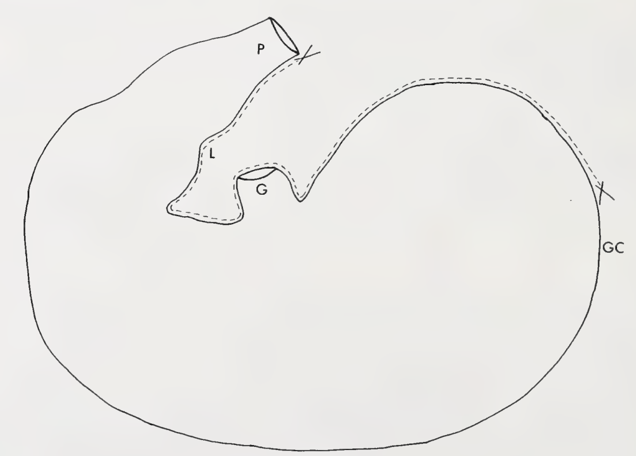
Nine vervet monkeys (4 adult males, 5 adult females) and eight samangos (4 adult males, 4 adult females) were shot on the farm Braco in the Karkloof area of Natal and used in this examination. Animals were weighed in the field and body lengths were measured from tip of nose to tip of tail. Gastrointestinal tracts were removed immediately. These were examined in the laboratory 2–3 hours later, which allowed for complete relaxation of the musculature in the GIT wall. No specimens were fixed prior to measuring, as this can cause distortion of the tract wall.

Measurements of the stomach, small intestine, caecum and colon, completely cleared of all mesenteric tissue, were made in a water-filled 2 m × 0.5 m × 0.1 m basin. Measuring the length of the gut under water minimises stretching, and is especially important when measuring small intestinal length. Small and large intestines were treated as cylinders and volumes were calculated from mean measurements of length and circumference. Width varies along the length of intestine, and at least 5 measurements of width (of intact tissue) were taken at regular points along the length. At a calculated mean width the tissue was opened and the circumference was measured. The surface area of the small intestine was also calculated from length and circumference measurements.

To calculate the volume of the caecum, an incision was made dorsally from the ileocaecal junction to the apex of the caecum. The contents were then flushed out and the lateral walls of the caecum were flattened into an approximate cylindrical shape. The length measurement and average circumference could then be taken and the volume calculated as for the colume of a cylinder.

Accurate measurements of stomach volume were difficult to obtain, largely as a result of its irregular shape and size in different animals. In most animals the length of the intact stomach was measured. It was then opened up along the lesser curvature from the gastro-oesophageal opening to the pyloric sphincter, and the incision was extended dorsocranially along the greater curvature for approximately 3 cm (Fig.). The stomach could then be opened out (flattened), the circumference measured and the volume calculated as for the volume of a cylinder.

Two other methods used, a. estimation of stomach volume by filling it with water and b. calculation of stomach volume from the greater curvature measurement (Chivers and Hladik 1980), were found to be unacceptable and were discontinued. Previous comparative work on primate GIT morphometrics involved use of length and width measurements of intact organs (Jones 1970; Milton 1981). Preliminary work in this study included this method, but these measurements were found to be unacceptable. Firstly, the varying thickness of gut musculature means that simple width measurements are mostly inaccurate (often by more than 1 cm). Secondly, the degree of stomach (or intestinal) fill, or the time elapsed since feeding, mean that stomachs of essentially similar size can provide very different measurements depending on when (time of day) they were collected. It is essential that measurements be taken only of dissected sections of the GIT with the contents removed. This negates the effects of varying muscle thickness (because measurements are taken on the mucosal surface of the gut), and is likely to provide more consistent results independent of whether the animal has recently fed or not.



Diagrammatic representation of a stomach, showing the incision made before stomach is opened out (flattened) and measured. P = pyloric sphincter, L = lesser curvature (gastro-oesophageal opening to pyloric sphincter), G = gastro-oesophageal opening, GC = greater curvature (gastro-oesophageal opening to pyloric sphincter)

To compensate for the effect of the larger body size of samangos, volumes of regions of the GIT in each animal were divided by the metabolic live mass ($mass^{0.67}$) of that animal. This provides a ratio that enables direct statistical comparison between species of the volumes of specific regions of the gut. Data were analysed using the Mann-Whitney two sample rank testing procedure (Zar 1974).

Results

Table 1 compares the measurements of volumes of stomach, small intestine, caecum and colon of adult (male and female) samangos and vervets. The mean body mass of samangos significantly ($P < 0.05$; Mann-Whitney U) exceeds that of vervets (males 8.33 kg : 5.58 kg; females 4.93 kg : 3.82 kg). Table 2 presents gut volumes corrected for differences in body mass of the two species, and includes significant differences in GIT volumes.

Table 3 shows small intestinal surface areas of males and females in each of the two species, and includes significant differences in the surface areas, corrected for different body mass, between the two species.

Table 1. **Measurements of body length and mass, and of volumes of stomach, small intestine, caecum and colon in samango and vervet monkeys**
(Mean ± standard deviation)

	Length (cm)	Mass (kg)	Volume (cm^3) Stomach	SI	Caecum	Colon
Samango						
Adult males (n = 4)	143 ± 1.5	8.3 ± 0.3	265 ± 16	366 ± 45	106 ± 15	728 ± 62
Adult females (n = 4)	121 ± 2.1	4.9 ± 0.3	169 ± 27	325 ± 27	72 ± 5.4	642 ± 99
Vervet						
Adult males (n = 4)	109 ± 1.4	5.6 ± 0.5	194 ± 44	179 ± 54	34 ± 3.1	318 ± 53
Adult females (n = 5)	99 ± 1.6	3.8 ± 0.3	168 ± 24	148 ± 41	23 ± 8.4	179 ± 13

SI = Small intestine.

Table 2. **GIT volumes corrected for differences in body mass between samangos and vervets**
Volume of section of tract/metabolic mass of the animal. (Mean ± standard deviation)

	Volume (cm^3) Stomach	SI	Caecum	Colon
Adult males				
Samango (n = 4)	64.3 ± 3.3	88.5 ± 9.9[a]	25.8 ± 4.2[ab]	175.8 ± 12.9[ac]
Vervet (n = 4)	61.0 ± 10	56.0 ± 13.5[a]	10.8 ± 0.5[ac]	100.5 ± 13.9[ad]
Adult females				
Samango (n = 4)	58.3 ± 7.9	111.8 ± 11.6[ab]	24.5 ± 1.3[cd]	220.0 ± 29.1[d]
Vervet (n = 5)	68.4 ± 8.0	60.2 ± 15.8[b]	9.2 ± 3.1[bd]	73.2 ± 6.6[cd]

Values with common superscripts in columns differ significantly using Mann-Whitney U ($P < 0.05$); SI = Small intestine.

Table 3. **The mean surface area of the small intestine in samango and vervet monkeys, including correction for the different body mass of the species**
(Mean ± standard deviation)

Species			Surface area (cm^2) actual	corrected
Samango	male	(n = 4)	1163 ± 122	281 ± 27[a]
	female	(n = 4)	1111 ± 48	382 ± 26[ab]
Vervet	male	(n = 4)	692 ± 87	217 ± 21[a]
	female	(n = 5)	595 ± 92	242 ± 33[b]

Values with common superscripts differ significantly using Mann-Whitney U ($P < 0.05$).

Discussion

Vervets and samangos occur syntopically in the Karkloof, and the same food resources were therefore available to both species. This was considered important because of the propensity of the gastrointestinal tract to undergo adaptive changes in relation to forage quality in different areas. These adaptive changes related to dietary variation are well documented (Poksey and Schneeman 1983; Gross et al. 1985; Perrin 1987). Similarly, in this study it was noted that culled vervets from marginal habitats had stomachs which were significantly smaller than those from the Karkloof area. It therefore seems important that comparative GIT measurements be taken on species occurring in sympatry, where the effects of food quality in different habitats would not affect gut morphology or capacity, and where different species are able to specialise on their preferred diets.

Only adult animals were used to obtain the comparative morphometric data. (There were large variations in intraspecific measurements of juvenile and subadult age-classes.) The importance of different organs might vary according to animal age and organ function (Johnson and McBee 1970; Bruorton and Perrin 1988), and it was concluded that only GIT measurements from adult animals would provide consistent and valid results.

There were no significant differences in stomach volumes between the two species. Both have a simple unilocular glandular stomach (Bruorton and Perrin 1988), which is characteristic of Old World cercopithecines (Hill 1958, 1966). On the basis of their similar morphology and function, it is perhaps to be expected that minimal size variations should occur between the two. Milton (1981) showed that stomach size of two sympatric primates in Panama, one highly folivorous *(Alouatta palliata)* and one highly frugivorous *(Ateles geoffroyi)*, were approximately equivalent. This is supported (for *Alouatta* and *Ateles*) by Hladik (1967) in his work on the relative surface area of sections of the digestive tracts of 24 primate species. Schieck and Millar (1985) showed that it is the distal parts of the digestive tract (caecum and colon) that correctly indicate diet type within rodent families. It appears, therefore, that stomach volumes remain fairly constant relative to body weight within primates possessing simple stomachs, and that differences in GIT volumes related to dietary adaptations would be found in other sections of the digestive tract.

Significant differences in small intestinal surface area existed between both males and females of the two species. This finding is not entirely consistent with previous work on other species. Schieck and Millar (1985) stated that small intestine lengths did not accurately reflect the amount of fibre in the diet of the 35 small mammal species they examined. Similarly, Milton (1981) and Hladik (1967) showed that small intestinal surface areas of the sympatric primates *Alouatta palliata* and *Ateles geoffroyi* (even with their extremely different diets) were approximately equivalent. Jones (1970) also found that relative lengths of the small intestine were fairly constant among the eight African

cercopithecids he studied. However, Chivers and Hladik (1980) showed, by regressing surface area of small intestine against body size, that absorptive surface area increases proportionately with metabolic body mass. The generally larger areas of small intestine in samangos might therefore simply be a factor of their larger size. Also, the consistently larger (relative) surface area in adult females (than males) might be related to the greater energy demands of the female during pregnancy and lactation, which are known to cause an increase in both small intestinal length and water content (Cripps and Williams 1975; Gross et al. 1985).

The caecum and colon of samangos were highly significantly more voluminous than those of vervets. This finding of greater caecal and colonic lengths and volumes in the more herbivorous species is well supported by previous studies. Schieck and Millar (1985) reported that colon lengths and weights represented diet types well, with herbivores having relatively larger large intestines than granivores and omnivores. Jones (1970) found that in eight cercopithecids the more folivorous species possessed relatively greater colon lengths, and in some cases greater caecum length. Similarly, Milton (1981) showed that the folivorous *Alouatta palliata* possessed a longer colon (double the surface area) than the frugivorous *Ateles geoffroyi.*

The caecum of herbivores is also generally larger than that of granivores or omnivores (Schieck and Millar 1985), and functions in the microbial conversion of fibrous material into compounds that can be absorbed by the colon (Sharkey 1971). Evidence for the importance of the caecum of the samango in fermentation has already been presented (Bruorton and Perrin 1988). A further study has also shown high concentrations of organic acids, as well as numerous bacteria, within the caecum and colon of both samangos and vervets.

It might be expected that the larger volumes of caecum and colon in the more folivorous samangos confers some selective advantage over vervets with respect to microbial digestion of leaves and other fibrous material. This would occur if the greater volumes were found to be important in food retention (or decelerating the passage rate of fibrous material), or if different species of fibre-digesting bacteria were present in one of the species. However, Clemens and Maloiy (1981) and Clemens and Phillips (1980) have shown that passage rates of food in vervets and in Sykes monkey *C. mitis kolbi* are extremely similar, with vervets retaining some particulate markers for longer time periods than did Sykes. They also suggest that food retention is not necessarily an important factor for the accumulation of organic acids, as high concentrations were observed in the colon of the bushbaby *Galago crassicaudatus* (Clemens and Maloiy 1981), which is smooth and non-complex and permits rapid passage of digesta. It is also suggested that herbivorous primates do not necessarily hold a fermentative advantage over omnivorous primates (Clemens and Phillips 1980), and that GIT structure does not appear to influence the concentrations of organic acids found in the mammalian hindgut.

Any advantages conferred by larger hindgut volumes are probably related to fermentation capacity in the two species. The larger the volume, the greater the amount of organic acids which may be produced by the microbial populations. Thus, even though the concentrations of organic acids in the hindgut of the two species are similar, the larger caecum and colon of the samango allows for greater production of these important microbial degradation compounds. Volatile fatty acids are rapidly absorbed by the large-intestinal mucosa of a wide range of mammalian species, usually at a rate similar to that determined for rumen epithelium (Rerat 1978; Stevens et al. 1980). However, the quantity of organic acids absorbed by the large intestine of a given species depends primarily upon the surface area available (Stevens et al. 1980). With the high component of leaf material in their diets, the extensive hindgut regions of samangos are, therefore, not only important in allowing a greater production of organic acids, but also for the greater absorption and assimilation of these important fermentation end-products.

Acknowledgements

We would like to thank the Natal Parks Board for issuing us with permits to collect 10 samangos. MRB thanks the Foundation for Research Development (C.S.I.R.) of South Africa for a bursary during the course of his study, and both authors thank the University Research Committee of the University of Natal for funds granted during the course of the study.

Zusammenfassung

Vergleichend-morphometrische Untersuchungen am Verdauungskanal von Grünaffen (Cercopithecus aethiops) und Diademaffen (C. mitis)

Vergleichend-morphometrische Untersuchungen am Verdauungskanal von Grünaffen und Diademaffen zeigten, daß Diademaffen wesentlich größere Raumanteile im hinteren Darm (Caecum und Colon) besitzen. Die Hauptabsorptionsoberflächen des Verdauungskanals (das Ileum) zeigte bei Diademaffen ebenfalls größere Ausdehnung als bei Grünaffen. Diademaffen fressen grundsätzlich mehr faseriges Laubmaterial als Grünaffen. Die Bedeutung der größeren Darmräume wird im Hinblick auf den Gärungsprozeß, der zu Aufbereitung und Verdauung dieses Laubbestandteils nötig ist, diskutiert.

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Testicular cycles of the Ringtail, *Bassariscus astutus* (Carnivora: Procyonidae)

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Abstract

Annual variation of testes in *Bassariscus astutus* was studied by palpation and morphological technique. Seasonal changes of spermatogenesis and testicular weight/size were compared. It could thus be confirmed that in Arizona the mating season extends from late winter into spring and that testes become aspermic in summer and reach their smallest size in autumn.

Introduction

The purpose of this study is to ascertain the annual cycle (seasonal development and regression) of the testes in *Bassariscus astutus*, and the determination of the male's ability (or inability) to produce active spermatozoa throughout the year. Ringtails appear to be seasonally monestrous, with the mating season extending from about mid February to May as evidenced by the majority of litters occurring during May and June (Grinnell et al. 1937; Poglayen-Neuwall and Poglayen-Neuwall 1980; Taylor 1954; Toweill 1976). There exists, to date, no histological study supporting this assumption.

Material and methods

Subjects and context

Thirteen wild-caught males were palpated at the time of capture and released while 23 captive males, ages ranging from 1 to 7 years, were palpated bi-weekly throughout the year to determine the size of the testes. In addition, 21 pairs of testes were taken from sacrificed animals, trap casualties, and fresh road kills. These were acquired for each month of the year. Ages of the animals, if not known, were estimated by tooth wear and by the morphology of the baculum (after Wood 1952). Testes were excised, and after removal of the tunica vaginalis, weighed (including epididymis) to the nearest 0.01 g. The greatest length and width (exclusive epididymis) were recorded to the nearest 0.01 mm. Each testis was hemisected longitudinally. Of each pair one testis was fixed in 10 % phosphate-buffered formalin of pH 7-0, for light microscopy. The other was fixed in a combination of 4 % commercial formaldehyde and 1 % glutaraldehyde in a buffer of 176 m/O/sm/liter (McDowell and Trump 1976) for electron and/or light microscopy. Specimens for electron microscopy were not available from the months of January, September und October.

Histological methods

For light microscopy longitudinal slices of the formalin-fixed testicle were cut, dehydrated and embedded in paraffin. Sections were cut a 5 μm and stained with hematoxylin and eosin. For transmission electron microscopy blocks no larger than 1 μm in any dimension were cut from the most superficial tissue, postfixed in 2 % OsO_4 in phosphate buffer, pH 7.4 for 1 hour, dehydrated in an ascending series of alcohol and propylene oxide and embedded in an epon-araldite mixture (Mollenhauer 1963). These sections were cut with glass knives, mounted on naked copper grids and stained with uranyl acetate and lead citrate.

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Seminiferous epithelial area (SEA) (BASURTO-KUBA et al. 1984) was estimated by photographing randomly selected seminiferous tubules at a magnification of ×50. Photographic prints were made to give a final magnification of ×425. Photographs were taken with a Nikon camera with Nikon attachment AMF on a Nikon labophot microscope. The basal membrane and the luminal margin were delineated to include all epithelial cells in 15 to 40 approximately round tubules in each animal. Coordinates of the seminiferous tubules were then digitized using a BQ CAM microcomputer system (R. and M. Biometrics, Inc., 5611 Ohio Ave., Nashville, TN 37209). The epithelial area of each tubule cross section was determined as the area inclosed by the basal membrane minus the area of the lumen. The SEA of each animal was expressed in square mm as the mean of the tubules measured. Student's t-test was used to test significance of differences between animals.

Five degrees of activity using a scale of 0 to 4+ were used to characterize sections of each testicle. For spermatogenesis in seminiferous tubules activity corresponded to the following: 0 = absence of sperm; 1+ = at least 1 sperm/sperm head; 2+ = several sperm/sperm heads; 3+ = moderate number of sperm/sperm heads; 4+ = many sperm/sperm heads. A similar scale was used to evaluate the number of sperm in the epididymis.

Results

Summary of the morphologic evaluation, morphometry (SEA) and statistical significance testing is indicated in Table 1. In late winter and early spring testes were most active. SEA was statistically low in December, January and February. A significant increase occurred in March, April and May and a marked decrease in June. From July to November testes were inactive. A rapid increasee in SEA between December and January was apparent.

The quantitiy of sperm in seminiferous tubules lagged 1 to 2 months behind changes in SEA (Table 1). Similarly changes in sperm concentration in epididymis usually was recorded a month later than in seminiferous tubules.

Table 1. **Spermatogenetic stages**

Month	SEA[1]	Sperm in sem. tub.	Sperm in epididymis
Jan.	8100	+ +	+ +
Feb.	7900	+ + +	+ +
Mar.	8500	+ + +	+ +
Apr.	4350	+ + + +	+ + +
May	4060	+ + +	+ + + +
June	4180	+	+ +
July	1900	0	0
Aug.	1680	0	0
Sept.	2560	0	0
Oct.	2040	0	0
Nov.	3190	0	0
Dec.	3250	+	0

[1] Calculated from the first day of each month.

Histopathological characteristics of the testis and epididymis are related to the stage of activity which correlated with the time of year (Figs. 1–5) and resembled those of other species in similar state of activity, e.g. Norway rat, rabbit, European boar and domestic cat (MOENS et al. 1975; MORTON et al. 1986; BASURTO-KUBA et al. 1984; ELCOCK et al. 1984). Degenerative changes occurred in the seminiferous epithelium during the period of declining activity, although there were a few stem cells present.

Weights of testes (Table 2) were lowest in September-October with steep increase toward March. Testes in March show maximum weight. From April to September the weight declines steadily. Similarly, linear measurements of testes show maximum length and width in March, and minimum length and width in September-October (Fig. 6).

Fig. 1. Seminiferous tubules representative of late winter and early spring (January). (×200)

Fig. 2. Seminiferous tubules of inactive phase. Sertoli cells predominate (September). (×200)

3

Fig. 3. Epididymis from most active phase of production (January). (×200)

4

Fig. 4. Epididymis from inactive phase (August). (×200)

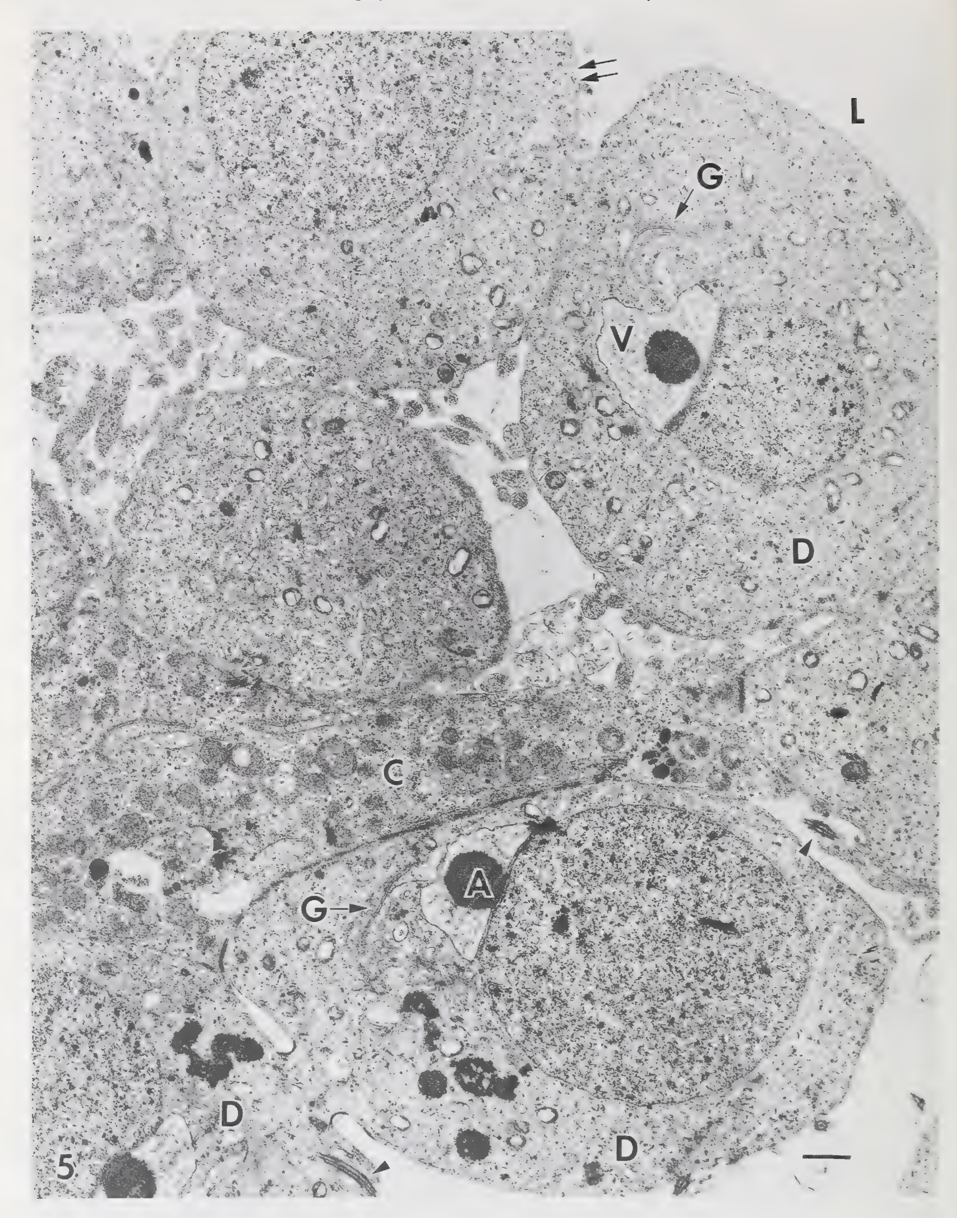


Fig. 5. Spermatids (D) at lumen (L) of active seminiferous tubule (February). Bar = 1 μm. The acrosomal vesicle (V) is at the nuclear membrane in 3 spermatids; it has not developed or is not in the plane of section in another spermatid (double arrow). The acrosomal granule (A) has not redistributed. Sacs of the Golgi complex (G) are in cytoplasm. Tangential sections of the principle piece of spermatozoa (arrowhead) occur. Part of a Sertoli cell (C) is included

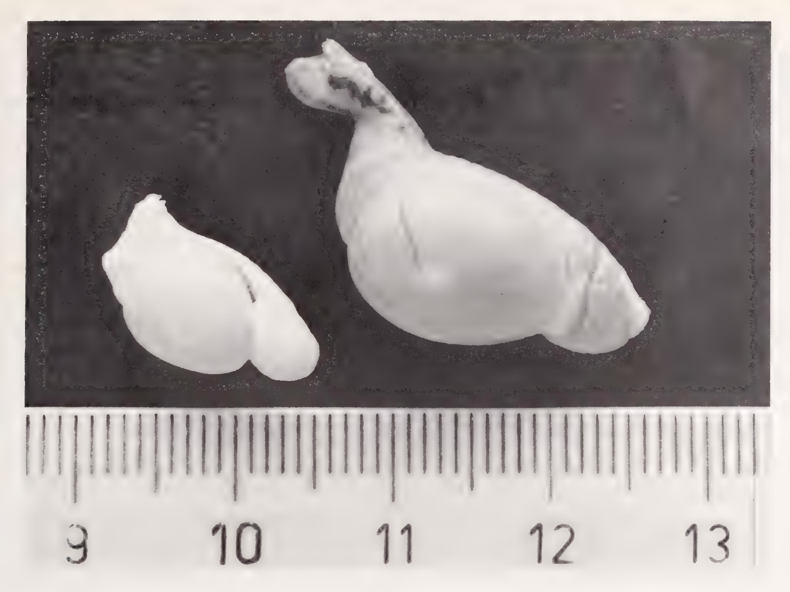


Fig. 6. Testes of *Bassariscus astutus*. *Left:* average size non-breeding season; *right:* average size breeding season

Table 2. **Weights (g) and linear measurements (mm) of testes**

Month	Weight	Length	Width
Jan.	0.96	13.92	10.62
Feb.	1.06	13.42	10.25
Mar.	**1.29**	**14.30**	**12.21**
Apr.	1.09	13.59	10.40
May	1.01	13.34	9.77
June	0.89	12.75	9.08
July	0.71	11.22	7.72
Aug.	0.45	10.51	6.90
Sept.	*0.36*	*10.38*	*6.70*
Oct.	*0.44*	*10.33*	*5.65*
Nov.	0.58	11.54	8.39
Dec.	0.61	12.16	9.16

Bold: maxima; italics: minima.

Measurements are means of left and right testes of a pair. Differences between left and right testis vary from 0 to 0.2 g and 0 to 1.7 mm.

Where more than 1 individual per month was available data were averaged.

Discussion

The physiological capacity to breed is characterized by the mass of the testis and the presence of sperm in the epididymis. The material described in this study clearly indicates an annual developmental cycle of redevelopment and regression of the testes of *Bassariscus astutus*. At age 16 weeks of the young, testes are tiny, ca. 4 mm diameter when descended and palpable, and from then on remain scrotal (Toweill and Toweill 1978). Although

there is no quantitative study, an unknown percentage of young males reach maturity at 10 months of age (POGLAYEN-NEUWALL and POGLAYEN-NEUWALL 1980; POGLAYEN-NEUWALL 1987) and thus are able to mate at or near the peak of the mating season. Of 5 yearling males, held in the senior author's colony, 2 have successfully bred; also 2 wild-caught young captured in March had large testes. Only 20 % of yearling male raccoons, according to WOOD (1955), possess motile sperm in the Texas post oak region. Among Michigan raccoons many yearling males are capable of reproducing, but females enter estrus about 2 months earlier, and by the time the young males are sexually mature most females are already bred by older males (STUEWER 1943). Active spermatogenesis of *B. astutus* is maximal during the late winter-spring mating season, while it rather abruptly diminishes in June and ceases in July. Our findings show that it takes 1 month plus for spermatogonia to mature to spermatozoa in ringtails, as compared with 20 days in rats (BLOOM and FAWCETT 1962), and 64 days in humans (DYM 1977).

The number of animals we examined resulted in maximum testis measurements for March, with most active spermatogenesis in April. A broader sample most likely would show a closer correlation between the two. We found the degree of testicular regression in *B. astutus* to be similar to that in *Procyon lotor* (SANDERSON and NALBANDOV 1973; WOOD 1955), and not nearly as stiking as in *Mustela frenata*, whose testes are 1/8 of their maximal size during the peak of their non-breeding season (WRIGHT 1947). Variation of testis size/mass correlated with the season is known in many mammalian species (AMANN 1970), e.g. *Martes americana* (MARKLEY and BASSETT 1942), *Mustela erminea* and *Vulpes fulva* (ASDELL 1964), *Dasypus novemcinctus* (MCCUSKER 1985), many cervids (AMANN 1970), several lemurs (BORART et al. 1977; PETTER-ROUSSEAUX 1972), *Saimiri sciureus* (DU MOND and HUTCHINSON 1967), *Macaca mulatta* (SADE 1964) and *Cercopithecus aethiops* on St. Kitts (CONAWAY and SADE 1969). The latter shows a distinct breeding season (different from that in Kenya), with a testis regression in the non-breeding season, which is much less pronounced than in the aforelisted primates. Sperm were present in the epididymides of all *C. aethiops* examined throughout the year (CONAWAY and SADE 1969).

The tropical *Bassariscus sumichrasti*, apparently a seasonal breeder, namely from January to May (GAUMER 1917; HALL 1981), does not show palpable testicular regression, as observed on 4 captive adults held by the senior author. No histological study of testes of *B. sumichrasti* has as yet been undertaken. Likewise *Ailurus fulgens*, a seasonal breeder, does not show cyclic variation of the testes' size (J. GITTLEMAN, comm. via g. CONOVER).

Electroejaculation on an adult *B. astutus* and an adult *B. sumichrasti* (conducted by Dr. B. DURRANT and the senior author in early May at the San Diego Zoo's Research Department) produced only minimal volume and very few, non-motile and mutilated spermatozoa. Likewise, electroejaculation on *Procyon lotor* was unsuccessful (SANDERSON 1951).

There is a correlation between daily sperm production and testicular weight for continuous breeders and for seasonal breeders during the breeding season (ORTAVANT, cit. by AMANN 1970). On the other hand MARTINET's (1966) quantitative, histological studies of *Microtus arvalis* revealed seasonality of the testes weight but there is no seasonal change in the efficiency of sperm production.

Sudden regression of testes during the mating season over a period of only very few weeks and concomitant decrease of active sperm has been noted by us in one newly captured *B. astutus*, perhaps as a direct result of the trauma suffered, and in 2 other ringtails probably as a consequence of constant harassment by a dominant female, which likely caused drastic hormonal changes conducive to the aforementioned reproductive condition. These 3 animals have not been considered in this study.

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Zusammenfassung

Testicularzyklen des Katzenfretts, Bassariscus astutus (Carnivora: Procyonidae)

Mittels Palpierung und morphologisch-histologischen Techniken wurden die Testes von *Bassariscus astutus* im Jahresablauf untersucht. Jahreszeitlicher Wechsel der Spermiogenese wurde mit Gewicht und Größe der Testes verglichen. Es konnte bestätigt werden, daß die Fortpflanzungsperiode in Arizona von Spätwinter bis in den Frühling dauert, und daß die Testes im Sommer und Herbst inaktiv (aspermisch) sind. Sie erreichen ihre kleinsten Maße im Herbst.

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Sexual bimodality in some recent pig populations and application of the findings to the study of fossils

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Abstract

Studied the size differences in some skull and tooth measurements between males and females in recent Suidae.

In three populations of *Sus* the linear measurements of the cheek teeth of the females ($0 \leq n \leq 25$) are on average 97 % those of the males ($0 \leq n \leq 28$). There is much overlap between the sexes. In *Babyrousa* such size differences are of the same order of magnitude. In an earlier study, using skull length, greater differences between the sexes were found. The value of skull length and some other skull measurements is discussed. Male Suidae have larger diastemas and longer skulls because of their larger canines.

The results of this study are applied to a sample of fossil *Bunolistriodon* from Córcoles (Guadalajara, Spain). The material is morphologically homogeneous, but there are two size groups differing on average by 15 %. There is no overlap between the groups. It is concluded that it is more likely that the material from Córcoles represents two species rather than males and females of the same species.

Introduction

A morphologically homogeneous collection of *Bunolistriodon* fossils from the Lower Miocene locality of Córcoles (Guadalajara, Spain) consists of two size groups, differing by 15 %. The question arose whether these groups represent two species or males and females of the same species. Usually sexual dimorphism in Suidae is apparent in the canines, but this criterion could not be used due to the state of preservation of the fossils. The present dilemma is not an isolated one in the study of fossil pigs (Pickford and Wilkinson 1975).

In some families sympatric morphologically similar species differ in size by 15 % (recent peccaries: Rusconi 1929; *Dorcatherium:* Mottl 1961; Fahlbusch 1985), whereas in other families males and females of one species differ by up to 13 % (Ursidae: Kurtén 1969; Torres 1984).

This paper deals with the size differences between males and females in recent pigs. The cheek teeth were measured as it is the intention to apply the findings to the study of fossils. In addition some skull measurements were taken.

Material and methods

Three collections of recent species, in which the canines indicate the sex of the specimen are studied. These collections represent approximately three populations, because they were made in a small area during a relatively short time. Not all measurements could be taken in all skulls, because of teeth that are not yet erupted or because of damage. The number of measurements taken are given in the tables.

The largest population measured is one of *Sus scrofa vittatus* from the former residence Deli, Sumatra, now called Sumatera Utara. The collection is stored in the Zoological Museum of Amsterdam (ZMA). The lower cheek teeth were measured and several skull measurements were taken. Males and females are about equally represented. The males are on average younger, in many the M_3 is not yet erupted or the talonid is still partly covered by bone (such individuals are considered to be subadults).

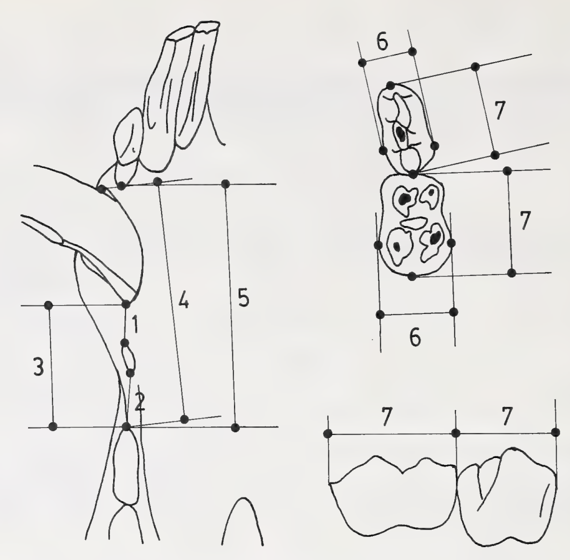


Fig. 1. The way of measuring. Diastemas and distances measured as the shortest distance between alveoli: 1. diastema C–P_1; 2. diastema P_1–P_2; 3. distance C–P_2; 4. distance P_2 – front of canine; 5. distance I_3–P_2; 6. DT, the greatest width (either measured at the anterior or at the posterior lobe) and 7. DAP, the greatest length of a tooth. (Measurements are in mm)

A smaller sample of *Sus barbatus* from east Bulongan, Borneo in the ZMA consists mainly of skulls without mandibles.

Sus verrucosus was measured in the ZMA and at Leyden in the Rijksmuseum voor Natuurlijke Historie (RMNH). Only specimens with a label indicating the provenance of Java were used. The females are underrepresented. No attempt has been made to measure all male material, which is very abundant. Most of the females of this species in the RMNH, also those which do not have a label specifying the provenance, do not have a fully erupted M_3. But most of the males are fully adult.

In addition data on recent *Babyrousa* from Bumbulan (females $3 \leq n \leq 5$, males $12 \leq n \leq 13$) and Buru (females $2 \leq n \leq 3$, males $13 \leq n \leq 16$) were taken from GROVES (1980).

The fossil *Bunolistriodon* material ($0 \leq n \leq 5$) will be compared to the recent material. It is stored in the geology department of the Universidad Complutense in Madrid and it is under study by V. D. MADE and ALFÉREZ.

Measurements of diastemas and the length of the skull are given for *Sus scrofa* only, as it is the largest sample.

Length and width of the cheek teeth and length of diastemas were measured as indicated in figure 1. Skull length was measured in the median plane from the tip of the nasalia to the posterior edge of the occiput. All measurements are in mm.

The value Q is introduced to express the mean size of a character of the females relative to the mean size of the males. It is given as a percentage. Q = (mean females/mean males) × 100 %.

Results

Average lengths and widths of the cheek teeth of *Sus* are given in table 1. On average females appear to be only slightly smaller than the males. Q values show little variation in the large *Sus scrofa* sample ($92 \leq Q \leq 101$), the average value is 97. Q values in the *Sus verrucosus* sample show more variation ($88 \leq Q \leq 123$), the average value is 98. The average Q value for *Sus barbatus* is 97 ($87 \leq Q \leq 105$), for *Babyrousa* from Buru 95 ($93 \leq Q \leq 99$) and for *Babyrousa* from Bumbulan 101 ($94 \leq Q \leq 106$). The average Q value for all populations is 98. Although the only sample in which females are well represented is that of *S. scrofa*, it is striking that in none of the other samples the average Q

Table 1. **Average dimensions of the cheek teeth of *Sus***

DAP = greatest length; DT = greatest width; n = number of measurements taken. Measurements in mm

	P_1 Mean	n	P_2 Mean	n	P_3 Mean	n	P_4 Mean	n	M_1 Mean	n	M_2 Mean	n	M_3 Mean	n
Sus scrofa vittatus														
DAP females	7.7	11	11.1	24	12.2	24	13.3	25	14.9	11	19.1	23	32.9	17
DAP males	7.6	10	11.3	19	12.8	25	14.2	27	15.2	25	19.9	28	34.0	11
DT females	3.8	10	5.6	24	7.4	24	9.3	25	10.8	11	14.3	23	16.2	17
DT males	3.8	11	5.8	19	7.6	25	10.1	27	10.8	25	14.7	28	16.6	11
Sus verrucosus														
DAP females	7.6	1	10.0	1	13.3	2	15.8	3	16.2	3	22.2	3	39.0	1
DAP males	6.2	7	11.4	8	13.9	8	15.1	8	15.2	8	21.5	8	40.8	5
DT females	3.0	1	5.4	1	6.9	2	10.0	3	10.7	3	13.9	3	16.1	2
DT males	3.0	7	6.0	8	7.2	8	9.8	8	11.0	8	14.6	8	18.1	6
Sus barbatus														
DAP females					14.7	1	14.9	2	17.6	2	23.1	2		
DAP males					14.7	7	15.5	6	18.0	5	24.0	6		
DT females					7.7	1	9.7	2	13.2	2	15.4	2		
DT males					7.6	7	10.2	6	12.6	5	16.6	6		
	P^1 Mean	n	P^2 Mean	n	P^3 Mean	n	P^4 Mean	n	M^1 Mean	n	M^2 Mean	n	M^3 Mean	n
Sus verrucosus														
DAP females	8.0	2	11.9	2	13.4	3	12.5	3	16.0	3	22.4	3	34.0	1
DAP males	8.6	6	12.4	7	13.0	8	12.5	8	15.7	7	22.0	8	35.7	6
DT females	3.6	2	6.8	2	10.4	3	13.3	3	12.8	3	16.6	3	18.5	2
DT males	3.6	6	7.6	7	11.1	7	13.5	8	13.3	7	17.4	8	19.9	6
Sus barbatus														
DAP females			12.7	2	12.9	4	12.8	6	17.7	5	22.8	6	35.6	3
DAP males			13.5	6	13.5	7	13.1	7	18.2	6	24.5	7	34.7	4
DTR females			7.7	2	11.4	5	14.4	6	15.1	5	18.4	7	20.4	3
DT males			8.9	6	12.0	7	14.5	7	15.5	6	19.4	7	21.0	4

Table 2. **Dimensions of the diastemas and skull lengths (in mm) of *Sus scrofa vittatus***

		Distance					
		$P_1 - C$	$P_1 - P_2$	$C - P_2$	Front $C - P_2$	$I_3 - P_2$	Skull length
Subadult	minimum	1.4	0.0	9.9	23.1	23.6	257
(n = 7)	mean	3.0	2.9	13.5	25.0	27.6	275
	maximum	5.1	5.1	16.8	27.3	31.2	295
Adult females	minimum	0.6	0.0	9.2	13.0	24.9	270
($14 \leq n \leq 17$)	mean	3.5	2.1	13.3	25.0	29.0	297
	maximum	6.1	7.3	20.1	31.5	35.2	321
Subadult	minimum	4.6	1.0	13.9	25.2	28.2	277
($12 \leq n \leq 14$)	mean	6.0	3.8	17.6	31.6	32.5	298
	maximum	8.1	6.4	22.1	38.3	39.2	321
Adult males	minimum	0.0	1.0	13.9	27.9	33.6	299
($8 \leq n \leq 12$)	mean	5.3	5.6	18.7	37.5	37.4	320
	maximum	7.8	12.7	22.9	44.0	40.8	342
Means							
100 × (subadult males/adult males)		113	68	94	84	87	93
100 × (subadult fem./adult fem.)		86	138	102	100	95	93
Q subadults		50	76	77	79	85	92
Q adults		66	38	71	67	78	93

value differs much from the value of this sample. The smaller size group in the *Bunolistriodon* material averages 85 % of the larger size group.

Size overlap between the sexes of *Sus scrofa vittatus* is great, in none of the cheek teeth two concentrations are formed (figure 2). This is also the case in *Sus verrucosus* and *Sus barbatus.* The size groups are better separated in similar diagrams for *Bunolistriodon.*

The size of the diastemas is about twice as large in the males as in the females (table 2). Also the total distance between the last incisor and the P_2 is much larger. In a similar way subadults of each sex have lower values than the adults, although there are some exceptions.

The Q value for skull length is 94 % (table 2).

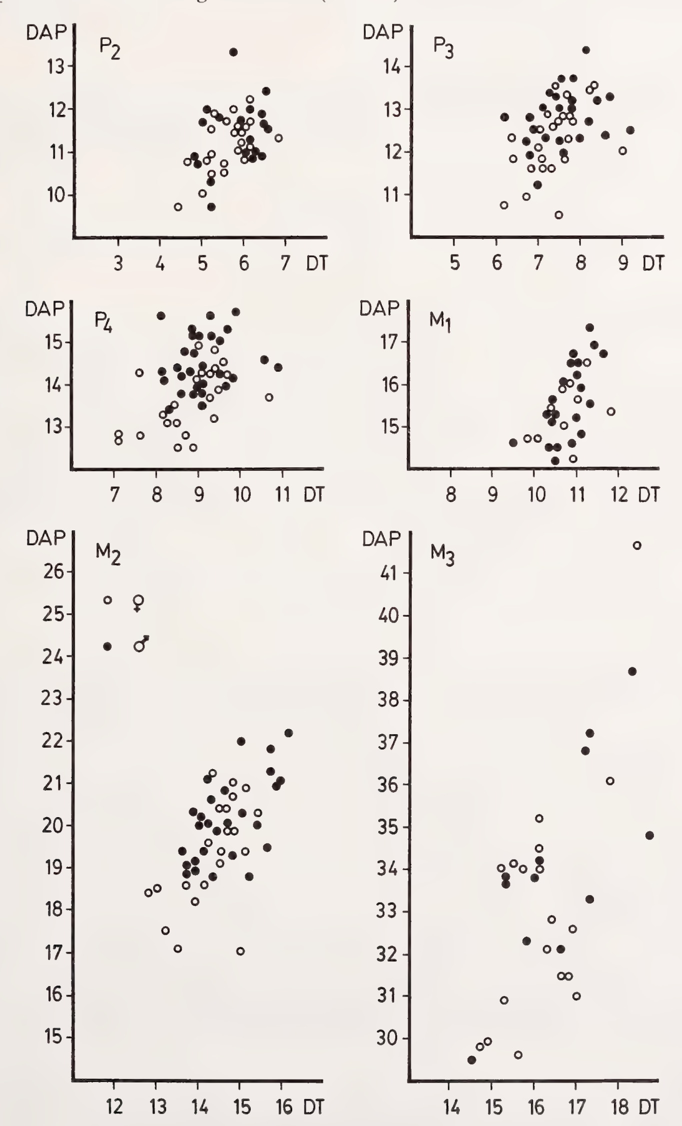


Fig. 2. Scatter diagrams for *Sus scrofa vittatus* from Deli. In the diagram for the M_3 a particularly large molar of which the complete width could not be measured is also given. (Measurements are in mm)

Discussion

The cheek teeth in *Sus scrofa* females are 97 % the size of the cheek teeth in the males. As the smaller samples do not differ in a substantial way (their average Q values vary from 95 to 101) the value of 97 % seems to be representative for the cheek teeth.

Average size differences between the sexes of 3 % only, seem to contradict the findings of GROVES (1981). He found that females averaged 85.4–95.3 of the males, 80.8–83.3 in *Sus verrucosus*. GROVES' values are based on the condylobasal lengths of the skulls. These measurements are roughly comparable to the skull length as measured in this study. The skull length includes the part with the canines; these zones are highly sexually dimorphic. The large *Sus scrofa* sample will be used to show how sexual dimorphism in the canine area causes a bimodality in skull lengths.

In the Deli sample the mean distance between I_3 and P_2 is 8.4 mm greater in the adult males than in the adult females; the difference for the skull length is 23 mm. If the males had no enlarged canines and diastemas their skulls would have an average length of 312 mm. The average female skull measures 297, which is 95 % of 312 mm. The dentition indicates a value of 97 %. So a large part of the size difference in female and male skulls is accounted for by the large canine zone in the males. In *S. verrucosus* diastemas tend to be much longer than in *S. scrofa* and in the small *S. verrucosus* sample size differences of the P_2–I_3 distance is 22.8 mm, which is much greater than in *S. scrofa*. So, a greater sexual bimodality in skull length is to be expected in *S. verrucosus*, although size differences in cheek teeth are not greater than in *S. scrofa*.

Part of the size difference for *Sus verrucosus* found by GROVES (1981) might be explained in this way, but the difference in length of the M_3 for *S. verrucosus verrucosus*, as listed by him, is large: females average 86 % of the males. My measurements indicate 96 % for the length of the M_3. There is no explanation for this discrepancy. It should be noted that for *S. verrucosus blouchi* the same value is 95 %. Also the standard deviation for the M_3 of the females of *S. v. verrucosus*, as given by GROVES (1981), is large. In any case, if an indication of size is needed for taxonomical purposes it is advisable to use a measurement that is less variable than skull length.

Sexually dimorphic canines influence both skull length and diastema length. Diastema length is used by some authors for taxonomical purposes (THENIUS 1972).

The difference in size of the diastemas in the females and males is related to the size of the canines. The larger the upper canines the larger are the diastemas behind the lower canines, and the same reasoning applies to the lower canines and the diastemas in front of the upper canines. As the canines of the males keep on growing (also their antero-posterior and transverse diameters increase) the diastemas have to grow too: the subadult/adult values for the distances C–P_2, front of canine – P_2 and I_3–P_2 are lower in the males than in the females (table 2). The continued size increase of the canines in the males seems to cause a decrease of the C–P_1 and C–I_3 distances, indicating that bone of the mandible is resorbed. The subadult/adult ratio for the P_1–P_2 (too high) and P_1–C (low) distances in the females is caused by a large number P_1 in contact with the P_2 in the adult females. The position of the P_1 seems to be variable.

The value of the size of the diastemas for taxonomy is restricted, as this character is related to sex and age and is influenced by the variable position of the P_1. If it is necessary to indicate the size of diastemas, it seems better to give the distance I3–P2 or the distance from the front of the canine to the P_2 in the mandible or the distance from the P^1 to the I^3 or I^2 in the upper jaw.

In the studied species the size difference between the males and females is small; in their direct ancestors this is probably also the case. Species of other subfamilies than Suinae are only known as fossils, so a study of this kind can be done for the Suinae only. The fact that size variation in large fossil samples is not greater than in recent species is an indirect

indication that large size differences between the sexes in fossil Suidae do not occur. Size variation in Suoidea will be subject to a separate study. Scanty fossil material of which the sex is known also indicates that there are no great size differences between females and males.

The presence of two species of *Bunolistriodon* in Córcoles instead of merely two sexes of one species, is likely because of:

1. The average size difference between the two size groups in *Bunolistriodon* from Córcoles is 15 %, which is much more than the 3 % of average size difference found in recent male and female Suidae.
2. The size groups are separated and do not have a large overlap as males and females of extant species.

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Zusammenfassung

Geschlechtsbimodalität bei einigen rezenten Schweinepopulationen und Anwendung der Befunde für das Studium an Fossilien

Diese Studie beschäftigt sich mit den Größenunterschieden zwischen weiblichen und männlichen Schweinen. In drei rezenten Populationen von *Sus* betragen die linearen Maße der Backenzähne der Weibchen ($0 \leq n \leq 25$) durchschnittlich 97 % derjenigen von Männchen ($0 \leq n \leq 28$). Bei *Babyrousa* liegen die Unterschiede in gleicher Größenordnung.

In einer früheren Untersuchung wurden bei Bezug auf die Schädellänge größere Unterschiede zwischen den Geschlechtern gefunden. Diese Studie stellt den Wert von Schädellängenmessungen und anderen Maßen zur Diskussion. Männliche Suidae haben längere Diastemen und längere Schädel wegen ihrer größeren Caninen.

Die Ergebnisse dieser Studie wurden auf eine Probe von Fossilen *Bunolistriodon* von Córcoles (Guadalajara, Spanien) angewandt. Dieses Material ist morphologisch homogen, aber in bezug auf die Größe können zwei Gruppen unterschieden werden. Der Unterschied beträgt 15 %, und es gibt keine Überschneidungen. Daraus wird geschlossen, daß das Material von Córcoles eher zwei Arten repräsentiert als die Geschlechter derselben Art.

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Dominance relationships and competition for resources among chamois *Rupicapra rupicapra rupicapra* in female social groups

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Abstract

Studied in a region in the Bernese Oberland (Switzerland) which animals in social groups of female chamois *Rupicapra rupicapra rupicapra* are able to assert themselves in competition for resources (licks, resting and feeding sites), and how losers behave after an interaction. The older animals regularly asserted themselves against younger individuals. Within the class of adult females (with or without kids) certain animals regularly asserted themselves against others. The most striking behaviour on the part of the loser, after having been forced to give up a resource to which it had previous access, was urination directly following the interaction, as a result of the latter and as a possible sign of stress.

Introduction

Outside the rutting season, which occurs in November/December, chamois live separately with regard to sex. The female chamois form social groups consisting of adult and subadult females, yearlings (including males) and kids (Krämer 1969; Knaus and Schröder 1983). Even in nonhunted, local populations (e.g. in game reserves) the number of animals remains fairly constant over a longer period of time, migration occurring only very rarely (Krämer 1969; Knaus and Schröder 1983).

These findings aroused the suspicion that social processes could play an important role in limiting population density (Krämer 1969). Later on, some indications supported this suspicion (Berducou and Bousses 1985; Lovari and Rosto 1985). Lovari and Rosto (1985) showed, that younger female chamois had a lower bite rate in the presence of older (dominant) females, suggesting, that in the long run that could be a reduced food intake of young females, influencing e.g. winter survival and reproductive processes.

The aim of the present study was to investigate one aspect of this problem, in particular: 1. whether certain individuals assert themselves in the competition among licks, resting and grazing sites; 2. how the behaviour of losers is influenced by the winners of an interaction.

Study area and animals

The study was carried out in the Swiss Federal Game Reserve Augstmatthorn in the Bernese Oberland (Switzerland) in summer 1987. The study area lies on the north-west slope of the Augstmatthorn at a height between 1500–2100 m altitude. It covers a surface area of approximately 3 km^2.

It was possible to observe a maximum of 126 predominantly female chamois; approximately 61 adult and 26 subadult females and yearlings as well as 39 kids. Animals were allocated according to age classes, using as criterion the length of their horns in relation to ear length (Lovari 1985; Patterson 1988). Males (except for male yearlings) were seldomly observed in this area.

Every day many animals visited the apparently very attractive licks including 3 optimal licks, the remainder being less attractive (Marbacher 1989), which were spread over a small area. The fact that, as a rule, there were considerably more animals than licks led to very strong competition at these sites.

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Methods

The chamois were observed from May to October at a total of 90 days. Observations were made each day from morning to evening using the "behaviour sampling" method (Altmann 1974).

Aggressive interactions (e.g. advancing with lowered horns towards conspecifics) in connection with competition for resources, occurred at the few available licks, at resting sites and during grazing. In order to classify which individuals were able to assert themselves, the numbers of animals remaining compared to those leaving were recorded, during situations when an older animal approached a younger one within three body lengths or vice versa at the licks, at resting and grazing sites. The Fisher exact test was used for statistical analyses for a total of 250 events.

It was possible on two occasions to observe two groups of four adults with kids (individually identifiable by morphological features such as colour of coat) at the licks during a period of several hours and to determine which animal drove the other away.

The winner of an interaction took over the resource or continued to use it and the loser retreated a few meters, stopped and often began to urinate. In order to determine whether urination was indeed a result of having been driven away, we then proceeded as follows:
We recorded the time until any urination occurred over a period of 5 minutes, a. after an animal had been forced to leave a site, b. after an animal had left a corresponding site on its own accord. The comparison was made with the Mann/Whitney U-Test.

Results

Winner and loser in the competition for resources

At licks: In all combinations of the 4 age-groups there were significant differences in the number of animals leaving to those staying at the approach of an other animal (Table 1). Almost without exception the younger animals retreated when an older one approached, while in the opposite case the older ones stayed. Among the individually recognizable adult females with kids, the same animals always asserted themselves in the course of a series of interactions (except in the case of animals E and F; Fig. 1), i.e. the subdominant animals had to "involuntarily" leave the lick together with their kids (Fig. 1).

At resting sites and when grazing: In the combinations studied the result was the same as at the licks. In all combinations studied, younger animals retreated at the approach by older individuals but not vice versa (Table 1). In some cases certain adult females with their kids retreated from other adult females.

Urination by the loser as a consequence of the interaction with a dominant animal

The most striking behaviour of an animal that had been driven away was urination after it had retreated a few meters. Animals driven away from licks and when grazing urinated in about 95 % of the cases, those driven away from resting places in slightly less than 90 %. Those not driven away, if they had left the corresponding place "voluntarily", urinated in 79 %, 52 % and 56 % of the cases. The difference between animals driven away and those not driven away when grazing and at resting sites was significant (Table 2). The lack of a difference at licks was clearly due to the fact that animals that had been licking for some time as a rule urinate upon leaving the lick. In all three situations, however, urination occurred significantly earlier in cases where animals had been driven away than in voluntary departures, i.e. within a few seconds (Fig. 2).

Discussion

Competition does not only occur at the few attractive licks, but also at resting sites and during grazing. Older animals in general tend to assert themselves in certain situations against younger ones, as has already been mentioned elsewhere (Krämer 1969; Lovari

Table 1. **Frequency of animals (belonging to different age classes) winning or losing in competition for licks, resting and feeding sites**

OF = old female; YF = young female; YA = Yearling; sK = strange kid; K = kid; a = animal at the site; b = animal approaching; ns = not significant (Fisher exact test)

a	b	animal at the site remains	retreats	p
		at licks		
OF	YF	12	4	< 0.001
YF	OF	0	16	
OF	YA	12	0	< 0.001
YA	OF	0	25	
OF	sK	19	0	< 0.001
sK	OF	0	27	
YF	YA	8	0	< 0.001
YA	YF	0	7	
YF	K	2	0	< 0.05
K	YF	0	8	
YA	K	10	0	< 0.001
K	YA	0	12	
		at resting sites		
OF	YF	3	0	ns
YF	OF	0	2	
OF	YA	6	0	< 0.001
YA	OF	0	7	
OF	sK	7	0	< 0.001
sK	OF	0	7	
		at feeding sites		
OF	YF	1	0	ns
YF	OF	0	2	
OF	YA	6	0	< 0.001
YA	OF	0	13	
OF	sK	7	0	< 0.001
sK	OF	0	13	
YF	YA	2	0	ns
YA	YF	0	3	
YA	K	4	0	< 0.01
K	YA	0	5	

and Rosto 1985). However the same evidently also occurs among older females, and in particular among animals whose age difference cannot be readly determined (on the basis of the length of their horns). The kids of the respective mothers shared the advantage or disadvantage. For example, kids of dominant mothers could use a lick unhindered during the period that their mother used the resource and conversely kids of subdominant mothers were forced to leave a lick together with their mother.

Older animals and those dominant within their class of adults were thus privileged in the utilization of resources. At licks: The best licks (with respect to humidity, access, see

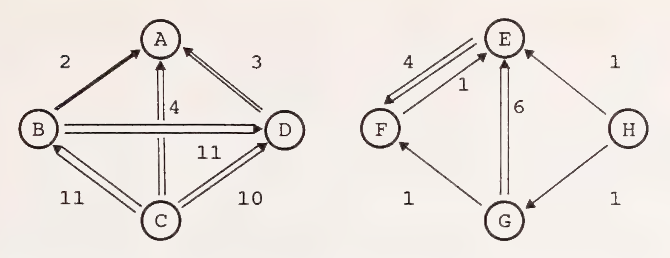


Fig. 1. Sociograms showing the number of successful approaches of adult females to other adult females staying at licks. A-H: Individually identifiable females with kids

Table 2. **Number of animals urinating after leaving a lick, a resting or a feeding site after** (a): it had been driven away or (b): it had left the site on its own accord; (+) = urination occurred; (−) = urination did not occur; ns = not significant

	at licks		at resting sites		at feeding sites	
	(+)	(-)	(+)	(-)	(+)	(-)
(a)	30	2	26	3	20	1
(b)	26	7	14	11	12	11
Chi-square	3.05		10.26		7.92	
p	ns		< o.ol		< o.ol	

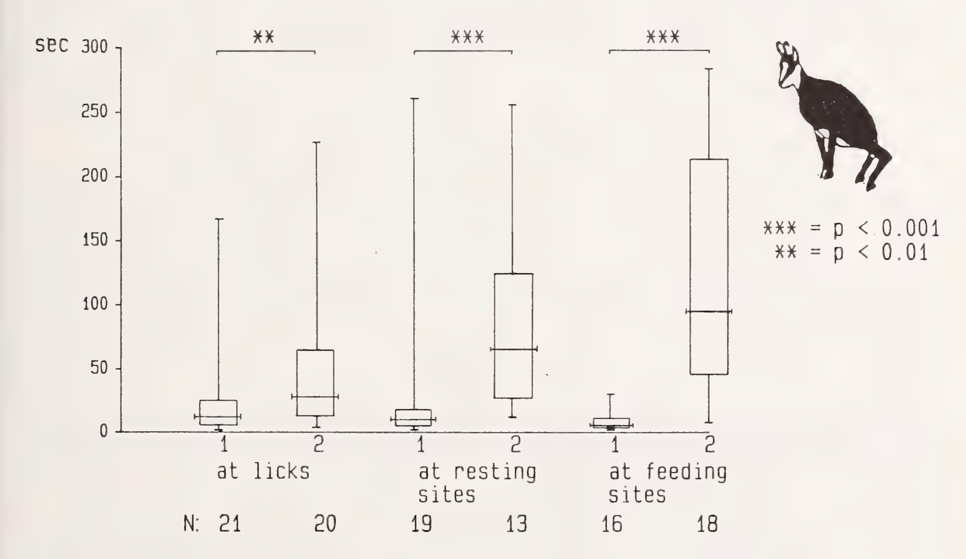


Fig. 2. Time until urination after an animal had been driven away or after it had left on its own accord at the licks, resting and feeding sites. Median, first and third quartil, minimum and maximum; 1 = driven away, 2 = left on its own accord (Mann/Whitney U-Test)

MARBACHER 1989) were mainly occupied by adult females with kids and as far as could be determined also by certain adult individuals without kids. At resting sites: Dominant animals occupy and retain desirable resting sites (e.g. shady sites during summer or at the very limited areas remaining snow in late spring), in contrast to subdominant animals. When grazing: Chamois eat selectively and have a particular preference for certain plants (KNAUS and SCHRÖDER 1983; FERRARI and ROSSI 1985; LEONI 1985). The fact that animals, after having driven away another one, continued eating at exactly the same place suggests that they fed on plants discovered by the previous animal. In individual cases this could be clearly ascertained. The distances between the chamois were small (a few body lengths on average; MARBACHER 1989) so that it can be assumed that they could see what kind of food their neighbour had been eating. It may be a question of special tactics on the part of the dominant animal, i.e. to keep an eye on what subdominant animals have found and to appropriate this at the expense of the others, as is said to be the case with Brent geese (DRENT, pers. comm.). It is quite possible that when grazing, subdominant animals are at a disadvantage, particularly when large areas are covered with snow or when snow remains for a long time.

It is striking that at the licks but also in a herd of grazing animals, short agonistic interactions occurred almost continuously. In such cases mostly younger, but also certain adult animals in the social group gave up resources, some of which they had discovered themselves and others that were well known resources (licks). Therefore they were probably almost always under a certain stress. The regularly occurring urination of an animal driven from a resource could be, in our opinion, the sign of such stress (some farm animals show enhanced defecation and/or urination under the influence of certain stressors, e.g. WOOD-GUSH et al. 1975). In any case it could be of importance as an indication of inferiority, as described in mountain sheep (GEIST 1971). Nevertheless, in the latter species it is thought to be a kind of submissive behaviour which prevents attacks from dominant animals. We have no indication for this theory in the present study. The dominant animal seems to be fixed on the resource, and pays apparently very little attention to the subdominant animal that has been driven away. There were virtually no observations of behaviour towards the urinating animal or to the urine itself (e.g. sniffing) within the herd of largely female animals studied (the only males were yearlings in this group).

More or less strongly pronounced stress leads to physiological responses which may change the function of the immune system, increasing susceptibility to disease (explored in some laboratory and farm animals, e.g. FRASER and BROOM 1990). Within social groups of female chamois it appeared that the social processes of competition for resources could have such an effect, especially under the circumstances of high population density. In order to examine this supposition, long-term studies on individually marked animals would be necessary.

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Zusammenfassung

Dominanzbeziehungen und Konkurrenz um Ressourcen in Gruppen von weiblichen Gemsen (Rupicapra rupicapra rupicapra)

In einem Gebiet im Berner Oberland, Schweiz, wurde im Sommer 1987 untersucht, welche Individuen in Gruppen von vorwiegend weiblichen Gemsen *(Rupicapra rup. rup.)* sich in der Konkurrenz um Ressourcen (Leckstellen, Liegeplätze, Nahrungsorte) durchzusetzen vermögen, und wie sich die Verlierer im Anschluß an eine Auseinandersetzung verhalten.

Generell setzten sich ältere Tiere gegenüber jüngeren Tieren durch und innerhalb der Klasse der adulten Geissen mit Kitzen regelmäßig bestimmte Tiere gegenüber andern.

Auffälligstes Verhalten der Verlierer, welche eine durch sie gehaltene Ressource aufgeben mußten, war Harnen unmittelbar nach der Auseinandersetzung als Folge davon und als möglicher Ausdruck von Streß.

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A contribution of the ecology of the Steppe pangolin *Manis temminckii* in the Transvaal

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Abstract

Various aspects of the ecology of the Steppe pangolin in the Transvaal are discussed. These include distribution outside the Kruger National Park, activity times and movement. Food and feeding are discussed as well as aspects of reproduction and growth. Mortality factors and Management problems, indicate the necessity for greater in-depth studies of these enigmatic animals.

Introduction

The Steppe pangolin *Manis temminckii* is probably one of the least known mammals in Africa in spite of its fairly extensive distribution from Sudan in the north to the northern Cape Province and Orange Free State in the south. Various authors (Smithers 1971, 1983; Dorst and Dandelot 1970; Kingdon 1971; Stuart 1979; Rautenbach 1982; Coulson 1989) have recorded the distribution and aspects of habits and feeding. Van Ee (1966) recorded the first successful breeding of this animal in captivity. An extensive account concerning the biology of pangolins including *Manis temminckii* was written by E. Mohr (1961). Despite these accounts the Steppe pangolin largely remains an enigma. This paper contributes towards the biology and ecology of the species in the Transvaal.

Materials and methods

During the period 1977 to 1983, 32 records of pangolins seen by farmers and Nature Conservators were examined by the senior author. In many cases the animals were confiscated from members of the public and returned to the sites of origin. In two cases the pangolins were rehabilitated at sites far from their original haunts with no success. These rehabilitations were monitored using transmitters.

A transmitter was also used to follow a single female on several farms in the Thabazimbi district for a period of two weeks. The transmitters used in all cases were SM1 type (AVM-Instrument Co.), and LA12 receivers (AVM – Instrument Co.) were used in tracking.

The radio transmitters were attached using fibreglass resin and steel (0,008 gg) wire. Four small holes were drilled through one of the large posterior dorsal scales (near the root of the tail). Two small loops were made with the wire which then held the transmitter to the scale. Liberal application of resin attached the transmitter firmly to the scale and gave excellent waterproofing. The trailing antenna was made from steel guitar wire (0,008 gg) and 45 cm long (¼ wave length, frequency 148 mHz).

Tracking was done on foot using hand-held yagi antennae. Monitoring of the rehabilitation animals started at dusk while that of the free ranging female continued as the animal became active, both day and night. During the tracking of this female, sites visited and fed at, were examined and the prey collected. These were then identified. The pangolins did not react to torch light and carried on foraging unconcernedly, allowing a relatively close monitoring of movement.

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Results and discussion

Distribution

The Steppe pangolin is widely distributed in the Transvaal being found in the bushveld areas of the western, northwestern, northern, north-eastern and eastern Transvaal. It is obvious from the frequecy of sightings that the western and north-western Transvaal are the stronghold of the species outside of the Kruger National Park, (Figure 1). Most sightings (69 %) were made between May and October possibly because it is easier to find them when the vegetation cover is least.



Fig. 1. Distribution of the Steppe pangolin *Manis temminckii* in the Transvaal, outside of the Kruger National Park during the period 1977 to 1983

Size and mass

Steppe pangolins in the Transvaal, are relatively small mammals reaching 1,3 m in length (nose tip to tail tip) but are most often between 0,7–1,0 m in length (Table 1). Males appear to be heavier and larger than females and there is a linear correlation between mass and length (Figure 2).

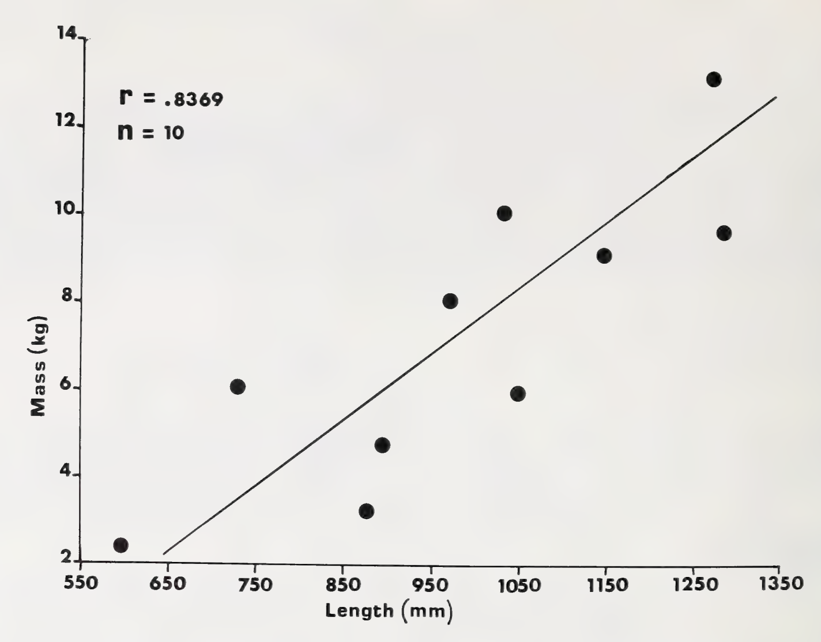


Fig. 2. Correlation between mass and length in the Steppe pangolin

Table 1. **Mass and size of Transvaal pangolins**
TL = Total length

	Mass (kg)	TL (mm)
Females		
	4.75	893
	4.68	–
	5.95	1040
	8.00	973
	10.09	1035
	Mean = 6.69	Mean = 988
Males		
	9.15	1150
	9.60	1289
	13.15	1275
	Mean = 10.63	Mean = 1238
Juveniles		
	0.39	–
	0.50	–
	2.40	595

Habits

Steppe pangolins are generally recorded as being nocturnal and partially diurnal animals (Smithers 1983; Dorst and Dandelot 1970; Kingdon 1971). According to recorded sightings and while radio tracking these animals it is apparent that they are crepuscular but forage into the night and even into the early hours of the morning, while also being found in broad daylight especially during the late afternoon. A summary of 17 pangolin sightings

by various observers in the Transvaal over a period of six years indicate a high frequency of activity (56 %) between 16h00 and 18h00. The remaining animals were observed at various times between midnight and midday.

An adult female translocated from the Vryburg District in the northern Cape Province and released on the farm Elandsfontein in the Thabazimbi District, Transvaal remained strictly nocturnal and moved about between 18h30 and 24h00, over a period of 10 days. Another female followed over a period of 18 days, initially followed a similar pattern of activity but changed its activity pattern repeatedly, becoming active in the early afternoon and sleeping by early evening (20h30).

The Steppe pangolin in the Transvaal spends these resting periods in available cover which is usually under a large rock, pile of stones, litter and vegetation. It has been suggested by BIGALKE (1932) and MOHR (1961) that these animals dig their own burrows as some of the Asiatic species do but this does not appear to be so. The only burrows used for shelter are those of antbears, *Orycteropus afer* and springhares, *Pedetes capensis* and in some cases hollowed out termitaria. These animals move over large distances inspite of their apparently clumsy mode of movement. The translocated female moved a minimum of 18.1 km over the 10 days of tracking. This averages 1.81 km day but as the animal was not closely followed this figure could be considerably larger. However, it agrees closely with the 50 m/minute recorded by BIGALKE (1932) for the Steppe pangolin in captivity.

Similarly the other radio-tracked animal which was released where found, appeared to travel on average a minimum of 0.7 km per day but as its meanderings were not measured, this could conceivably be as much as the first. As the translocated animal appears to have behaved atypically, more emphasis is placed on the animal released where it was found. This particular pangolin, a female travelled from the point of release up the side of a hill to the crest where it spent the next 10 days feeding and meandering about over a very small area (Fig. 3). Over the next five days it moved along the crest of the hill to another site where she spent a minimum of three days whereafter tracking was stopped. Another 18

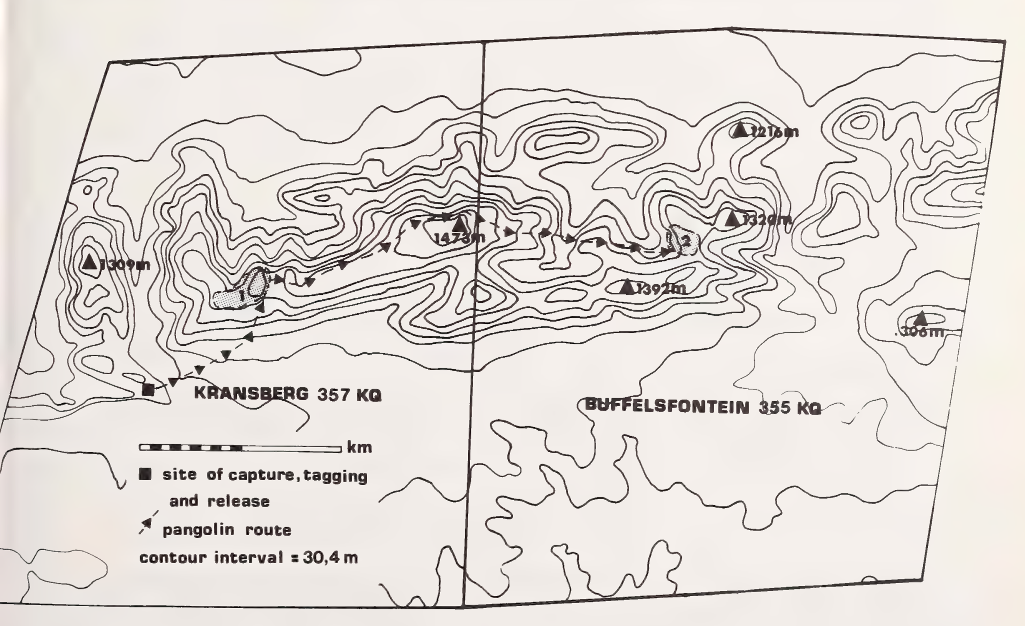


Fig. 3. Movements of a resident Steppe pangolin over a period of 18 days. The shaded areas 1 and 2 are where the pangolin foraged over 11 and a minimum of 3 days respectively

days later the signal from its transmitter was located in the close vicinity of where it was last seen.

It is apparent that the animal used a system of bases from which it foraged, obviously locating sufficient food on her excursions. In fact she was seen to forage in places where she had previously foraged. The foraging excursions were of relatively short duration ranging from five to six hours. When she went to ground she chose sites under and among boulders and stumps and in holes, on occasions using the same holes as she had on previous occasions and on other occasions new hiding places. One such site was used for seven days with the animal returning to it after each foraging excursion. On one hot day (28 March 1981) the female was observed to lie up in the shade of some small trees and rest. It was then observed to lie on its back and expose its bare belly. This was moist, whether from sweat or urine and permitted the animal to cool off. Such stops occurred on several occasions thereafter, lasting from a couple of minutes to as much as 1½ hours. It was noticed that all pangolins kept in captivity urinated on themselves squirting urine in short bursts.

This obviously has a cooling function but also permits the animal to advertise its presence to other pangolins as it moves about an area. This was confirmed while following the female on the farm Kansberg, where she was seen to leave wet marks on the rocks which she traversed. In addition, the urine has a pungent odour which is recognisable by humans and therefore even more pronounced to the smell sensitive pangolin.

Foods and feeding

Pangolins forage by walking slowly along sniffing in likely places. Once a nest of ants or termites has been located the pangolin rips open the nest with the short powerfully armed front feet. The exposed holes are sniffed at extensively and the tongue is only extended down those holes where there are large quantities of these insects, other holes are ignored. At each site the animal will remain still with its tongue extended down the hole and while the supply of ants continues. As soon as there are no more insects the pangolin will scratch at another site and the process repeated. In no case was a nest of ants or termites totally devastated and the raided colonies would quickly be able to rebuild the nests and numbers of the various castes consumed. Throughout this sniffling at the exposed holes of the ants nest the nose is continuously wet and at times the animal is seen blowing bubbles. The Steppe pangolin in the Transvaal feeds mostly on ants and termites expecially the former. Table 2 lists the species of ants and termites fed on.

Sweeney (1973) also records that this pangolin species in the Sudan and in Malawi fed mainly on ants but would only eat the larvae and eggs of *Camponotus maculatus* and *Crematogaster* sp. and not the workers. He also recorded that they would not feed on

Table 2. **Prey species of a free ranging Steppe pangolin in the Transvaal**

FORMICIDAE	
Acantholepis capensis	*Monomorium albopilosum*
Anoplolepis custodiens	*Myrmicaria natalensis*
Camponotus eugeniae	*Pheidole megacephala*
Camponotus thales	*Polyrhachis schistacea*
Camponotus sp.	*Tapenonia luteum*
Crematogaster amita	*Technomyrmex albipes*
	Xiphomyrmex weitzaeckeri
ISOPTERA	
Odontotermes badius	Termitidae – humus feeders
Trinervitermes rhodesiensis	(possibly *Alyscotermes* sp. or *Astalotermes* sp.)

Trinervitermes geminatus. In Malawi they were observed to eat worker driver ants, those of several *Camponotus* species and *Trinervitermes* sp. nymphs. The pangolins were reluctant to feed on *Odontotermes smeathmani* when the nest was unopened, but would eat these termites when the nest was artificially broken open. Sweeney (1973) also recorded that the pangolins never broke open nests of *Trinervitermes* and *Macrotermes* but ate the termites when these were found. The pangolin foraged for termites under cow pats and wood sometimes picking these up and holding them to the chest.

Although this last observation has not been observed in the Transvaal, it has also been found that pangolins do not break open *Trinervitermes* or *Macrotermes* nests but appear to concentrate on litter feeding termites and on those termites found away from the nest. They do, however, concentrate far more on ants of the family Formicidae as the accompanying table shows.

A large male Steppe pangolin defaecated, after being in captivity for approximately 60 h, 160 g of faecal material, largely soil but also some vegetation, sand, remnants of formicid ants and termites. There were even several stones measuring up to 9 × 3 mm. These are no doubt accidental ingestions. Another day later this animal voided a further 107.5 g of faecal material much the same as the last. Therefore this animal had ingested at least 267.5 g of food and secondary material prior to capture as no food had been consumed since.

Reproduction

The Steppe pangolin gives birth to a single neonate (Van Ee 1966; Smithers 1983; Mohr 1961; Coulson 1989). This was substantiated during the course of this study with one exception, that of a female, observed by H. Pettifer (pers. comm.) on the farm Tangala in the Transvaal lowveld, accompanied by two young of similar sizes which indicated that they were from the same litter. This would be the first recorded birth of twins in the species.

During the course of this study an injured female gave birth to what appears to be a premature neonate, in August. This neonate, born at the Onderstepoort Veterinary School, measured 22.5 cm in total length and had a mass of only 120 g.

During this study a 2.4 kg juvenile was seen to ride on the back of her 8 kg mother. The two juveniles observed by H. Pettifer above, had masses of 392 g and 510 g respectively while their mother had a mass of 4.74 kg.

Mortality

During the period of study, four pangolins were found dead or died subsequently from wounds inflicted by humans. Three of these were killed for consumption while the fourth was found shot with a shotgun for no apparent reason.

The only natural mortality was that of an adult male from the Farm Schietfontein 55 MS in the Messina district which was found by a farmer on the 7th August, 1983. Two days later it died and on investigation was found covered with mites (*Manitherionyssus heterotarsus*) and tampans (*Ornithodorus moubata*). According to Dr. Boomker (Parasitologist, Onderstepoort, pers comm.) these eyeless tampans were probably responsible for the pangolin's death by inducing progressive paralysis.

Management

On account of the number of pangolins brought in, some of which were relocated, it was desirable to determine whether such relocations work. Monitirung using transmitters was only carried out with two individuals one of which subsequently proved to have been injured by a knife or spear in the upper region of the hind limbs. In both cases the animals

were found dead 10 days after release. Mention has already been made of the female from Vryburg, while the injured animal came from the Thabazimbi District and was released at the Hans Strydom Dam Nature Reserve on top of the Waterberg. The female from Vryburg was found dead with the head and soft parts of the body consumed. Whether the death was a result of predation or stress could not be deduced as rains had obliterated any tracks. From the behaviour of this animal it is likely that relocations or translocations may be unsuccessful. Until more knowledge of this species' habits is acquired it seems wise at this stage to only attempt to relocate confiscated animals in those vicinities where they were initially found and not try to translocate them to nature reserves where their death could result.

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Zusammenfassung

Ein Beitrag zur Ökologie des Steppenschuppentieres Manis temminckii in Transvaal

Angaben über das Steppenschuppentier (*Manis temminckii*) in Transvaal werden zusammengetragen: Verbreitung außerhalb des Krüger-Nationalparks, Körperlängen und Gewichte, Aktivität und Ernährung. Die Bewegungen eines Weibchens wurden längere Zeit telemetrisch kontrolliert.

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Seasonal changes in reproduction and diet of the Bushveld gerbil, *Tatera leucogaster* (Muridae: Rodentia), in Zimbabwe

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Abstract

The reproductive ecology and diet of *Tatera leucogaster* were studied in two areas, mixed woodland and Miombo, in the Sengwa Wildlife Research Area, Zimbabwe. Both populations ceased breeding during the cool dry season but one population started breeding three months before the other. The two populations had similar diets, and rainfall and temperature were also similar in the two areas. The difference in duration of breeding in the two areas was probably related to food abundance.

In both study areas the testes mass of adult males made up about 6 % of their body mass. The adult sex ratio was strongly biased in favour of females during the breeding season.

In the mixed woodland area, females had an average litter size of 5.6 ± 0.29 and an annual reproductive capacity of 28 young per adult female. In Miombo, females had an average litter size of 4.8 ± 0.36 and an annual reproductive capacity of 12 young per adult female.

The diet mainly consisted of seeds (50–75 %) and insects (10–40 %), with a small amount of stem and leaf material (< 10 %). There was little seasonal variation in diet.

Introduction

The bushveld gerbil, *Tatera leucogaster*, is widely distributed throughout southern Africa (Smithers 1983) and has a variable pattern of breeding. It breeds throughout the year in Botswana (Smithers 1971) but mainly breeds during periods of high rainfall in Zambia (Chidumayo 1980) and the Transvaal (Perrin and Swanepoel 1987).

The main objective of the present study was to document the breeding biology and diet of *T. leucogaster* in two similar habitats separated from one another by a distance of 8–9 km. A comparison of the results from the two areas gives one an opportunity to separate the effects of climate (rainfall and temperature), which is similar in the two areas, from the more local effects of the abundance and availability of food. This approach is particularly useful if, as was the case in this study, the breeding seasons in the two areas are very different.

A second objective was to examine certain aspects of the reproductive biology of the males. Adult male *T. leucogaster* have extremely large testes during the breeding season (Perrin and Swanepoel 1987), similar to certain other species of *Tatera* which have the largest proportion of body mass allocated to testicular tissue known for mammals (Kenagy and Trombulak 1986). I examine the constancy of this feature within the genus and show how the size of the testes is correlated with adult sex ratios and regression of the testes during the non-breeding season.

Material and methods

Study areas

A total of 300 *T. leucogaster* were collected from a 4 km^2 area of the Samapakwa plateau (18°05′ S; 28°08′ E) during the period July 1987 to June 1988, and during the period November 1987 to June 1988 a further 145 animals were collected from a 2 km^2 area of mixed woodland adjacent to the four square mile area (18°10′ S; 28°10′ E) in the Sengwa Wildlife Research Area in Zimbabwe.

The Sengwa Wildlife Research Area is described by Cumming (1975). The study area on the Samapakwa plateau is Miombo (a *Brachystegia-Julbernardia* mixed woodland). The commonest trees were *Brachystegia boehmii, B. spiciformis, Julbernardia globiflora, Terminalia sericea, Combretum zeyheri*, and *Baphia massaiensis*. The shrub *Xeromphis obovata* was particularly common. Most of the larger trees had been destroyed by elephant a decade or so prior to my study but an elephant reduction program, which ended in 1982, has allowed a prolific regrowth of trees. To prevent a late dry season fire from destroying this regeneration of trees the area has been subjected to cooler annual burns at the beginning of the dry season. Consequently, herbs and grasses were sparse. Common grasses included *Eragrostis viscosa, E. curvula, E. cilianensis, Aristida adscensionis, A. pilgeri, A. vestida, Dactyloctenium gigantum, Heteropogon contortus, Leptocarydion vulpiastrum, Panicum maximum, Pogonarthria squarrosa, Schizachyrium jeffreysii, Schmidtia pappoporoides*, and *Setaria pallidifusca*.

The second study area was mixed woodland and bushland dominated by *Colophospermum mopane, Combretum apiculatum, C. zeyheri*, and *Erythroxylum zambesiacum*. The area was not burnt and so herbs and grasses were much more abundant than on Samapakwa. Common grasses included *Eragrostis viscosa, E. cilianensis, E. regidior, E. superba, Dactyloctenium gigantum, Chloris virgata, Urochloa trichopus, Digitaria eriantha, Andropogon gayanus*, and *Schmidtia pappoporoides*.

Rainfall and temperature were monitored at the Sengwa Wildlife Research Institute (18° 10′ S; 28° 13′ E). Monthly means were determined from daily records.

Collection and processing of animals

The two areas were sampled monthly by lines of snap traps placed at irregular intervals adjacent to burrows. Traps were left in place for two days and were then moved. Trapped areas were not retrapped. Animals were measured, sexed and weighed soon after removal from the traps. A clean mass was determined by removing the gut, from the lower oesophagus to the rectum, and also the uterus and embryos of pregnant females.

Seasonal changes in female reproductive activity were assessed as follows. First, females were classed as mature if they were reproductively active (see below) or had been in the past, i.e. had placental scars, otherwise they were classed as immature. Mature females were further categorized as 1. pregnant if they had implanted embryos; 2. reproductively active if corpora lutea were detected in the serially sectioned ovaries or if the uterus was distended with fluid (i.e. in proestrus); 3. remaining females were considered to be reproductively inactive. In addition, females were classed as lactating if milk could be expressed from their nipples. Note that it was possible for a lactating female to be categorized as reproductively inactive.

Seasonal changes in male reproductive activity was assessed in two ways. First the reproductive organs were dissected out and a sperm smear taken from each cauda epididymis. The abundance of spermatozoa for each smear was then quantified as 0 if none were present, 1 if only a few spermatozoa were present, 2 if spermatozoa were common but still scattered on the slide, and 3 if the smear mainly consisted of spermatozoa. An average sperm abundance could be determined for any group of animals. Secondly, the paired testes and seminal vesicles were fixed in Bouin's solution and weighed to the nearest 10 mg. To determine if the reproductive organs of adult males regressed during the non-breeding period the means of the log transformed mass of the testes and seminal vesicles were computed for monthly samples of males in age classes 4–8 (see below). This procedure largely eliminated changes resulting from a seasonal influx of juveniles into the population.

The number of litters and reproductive capacity (production of young per adult female) during the breeding season were calculated using the method described by Neal (1981, 1982). This method considers that the interval between litters is made up of a non-pregnant period (p_o), a pre-implantation period (p_l), and a post-implantation period (p_v) when embryos are macroscopically visible. The value of p_l was assumed to equal 4 d (see Neal 1981) and that of p_v was estimated as 24 d because the gestation period, which equals $p_l + p_v$, is 28 d (Chidumayo 1980). The average value of p_o could then be estimated by assuming that the ratio of $p_o + p_l$ to p_v was the same as the ratio of non-visibly-pregnant adults to visibly-pregnant adults. The average interval between litters could then be estimated. The average number of litters and production of young could then be determined knowing the duration of the breeding season and the mean litter size.

The relative age of individuals was estimated using the eruption and subsequent wear of the upper molars as criteria. Eight age classes were recognised, ranging from the condition when the third upper molar was not fully erupted (age-class 1) to the condition when all molars were worn to the state where no enamel was visible on the upper surface (age-class 8).

Stomachs were preserved in Bouin's solution before transfer to 70 % alcohol. The stomach contents of animals collected in the same month and area were combined and the composite samples were sent to the Composition Analysis Laboratory at Colorado State University for analysis by microhistological techniques. Details of the analysis are described by Neal (1984a, b). Food fragments were categorized into four classes: anthropod (mainly insect), seed, plant stem and leaf, and fungi or lichen.

Results

Climate

There were 909 mm of rain during my year of study compared to a yearly average of 670 mm during the previous 22 years. Prior to my study it had last rained on March 26, 1987 and until early February 1988 the monthly rainfall was below the long term average (Fig. 1) except for December 1987. Rainfall was considerably higher than the long term average during the period February–March 1988. Thus, the April–November dry season was longer and more severe than usual, and rainfall was heavier and more concentrated towards the end of the rainy season than usual.

The temperature also varied seasonally (Fig. 1), being at a maximum in November at the end of the dry season and beginning of the rains (mean monthly maximum of 37.0 °C; mean monthly minimum of 27.7 °C) and a minimum in July (mean monthly maximum of 27.0 °C; mean monthly minimum of 8.3 °C).

Thus, the year may be divided into three main seasons: a cold dry season from mid-May to mid-August when the daily maxima and minima averaged 27–29 °C and 8–11 °C respectively; a hot dry season from September to November when the daily maxima and minima averaged 34–37 °C and 17–22 °C respectively; and a warm wet season from December to April when the daily maxima and minima averaged 31–34 °C and 18–21 °C respectively. The precise timing of these seasons varies slightly from year to year.

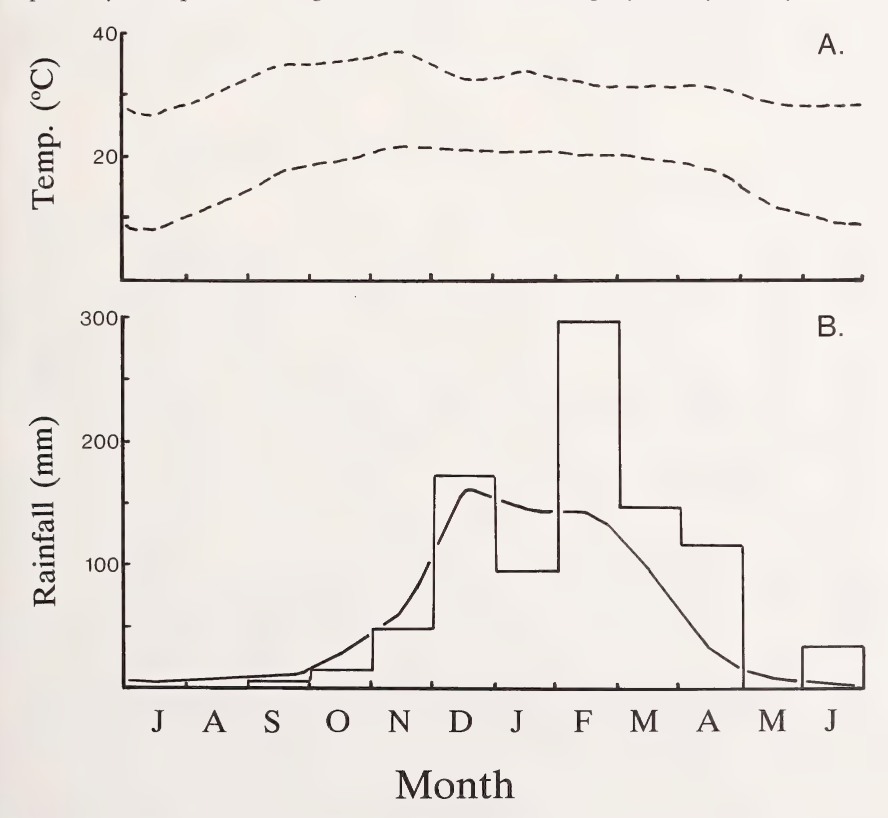


Fig. 1. A: Seasonal changes in mean monthly minimum and maximum temperatures (°C). B: Histogram of total monthly rainfall (mm) from July 1987 to June 1988. The average total monthly rainfall during the period 1965–1987 is also indicated

Body mass

The mean birth mass of 7 young born in the laboratory was 2.8 g (range 2.6–3.0 g) and they were weaned at a mass of 16–22 g at an age of 18–28 d (NEAL 1990). Individuals of both sexes usually attained sexual maturity at a body mass of 60–70 g. The mean body mass of 65 adult males was 79 g (range 58–113 g) and that of 191 adult females was 72 g (range 44–122 g). This slight sexual dimorphism of body mass is consistent with that reported in other studies of this species and for other species of *Tatera* (NEAL 1982). Adult body mass varied seasonally, reaching a maximum during the rains and early part of the dry season and declining to a minimum towards the end of the dry season. For example, parous, non-pregnant females in the Miombo habitat had a mean body mass of 61 g during September–November compared to a mass of 74 g during January–June and the body mass of adult males averaged 72 g and 83 g for the same two periods. Seasonal cycles in body mass have also been reported for *T. nigricauda* (NEAL 1982) and *T. afra* (ALLANSON 1958; MEASROCH 1954).

Sex ratios

The sex ratio of juveniles (i.e. individuals in the youngest two age classes) was not significantly different from parity both in mixed woodland (χ^2 = 1.1; $P > 0.2$) and Miombo (χ^2 = 0.4; $P > 0.5$). Similarly, the sex ratio of adults (i.e. individuals in age classes 3–8) was not significantly different from parity during the non-breeding period, May–November, in Miombo (χ^2 = 0.75; $P > 0.3$). In contrast, the sex ratio of adults during the breeding season was strongly biased in favour of females both in mixed woodland (χ^2 =

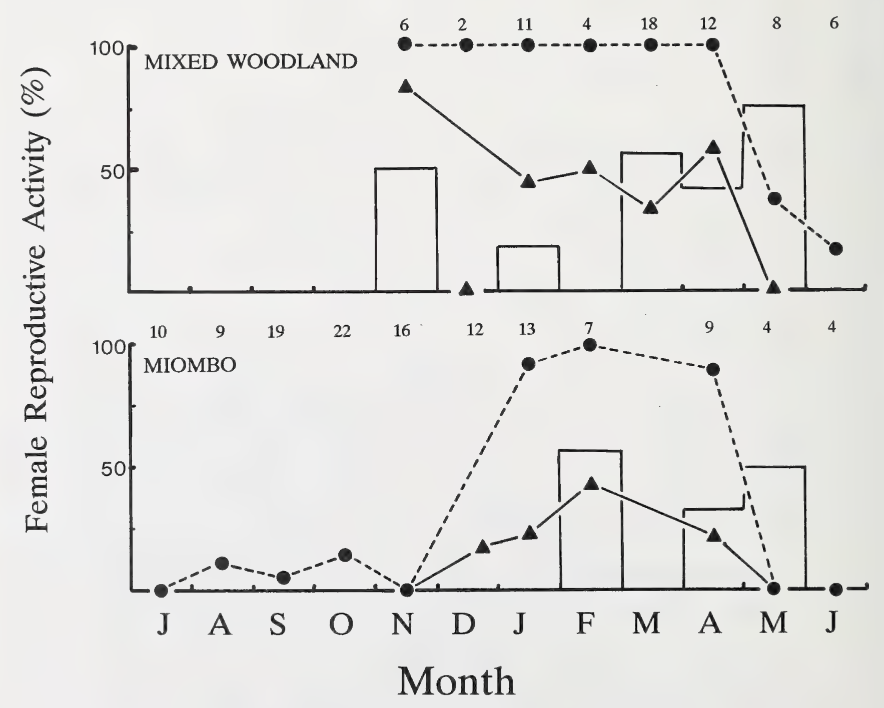


Fig. 2. Seasonal changes in adult female reproductive activity of *T. leucogaster* in two habitats. Percentage of adult females: 1. with corpora lutea or in proestrus (●----●), 2. with implanted embryos (▲—▲), and 3. lactating (histogram). Numbers represent sample sizes

12.2; $P < 0.001$) and Miombo ($\chi^2 = 5.7$; $P < 0.02$). Chidumayo (1980) has also reported 1 : 1 sex ratios for juveniles and subadults, but a significant excess of old females during the breeding season in *T. leucogaster* in Zambia.

Breeding season

Female breeding activity was seasonal (Fig. 2) and mainly confined to the period of rainfall. The breeding season was longer in the mixed woodland area than in Miombo. Pregnancies were first observed in Miombo during the latter half of December resulting from conceptions sometime after the first week of December. In contrast, when the area of mixed woodland was trapped for the first time during the latter half of November most females were pregnant and the presence of lactating females (Fig. 2) and young juveniles (Fig. 4) indicate that breeding had been in progress for at least two months. Thus, pregnancies occurred at least three months earlier in mixed woodland than in Miombo. Breeding in both study areas ceased coincidentally with the end of the rains at the end of April.

Adult testes mass and seminal vesicles mass were at a maximum during the rains and

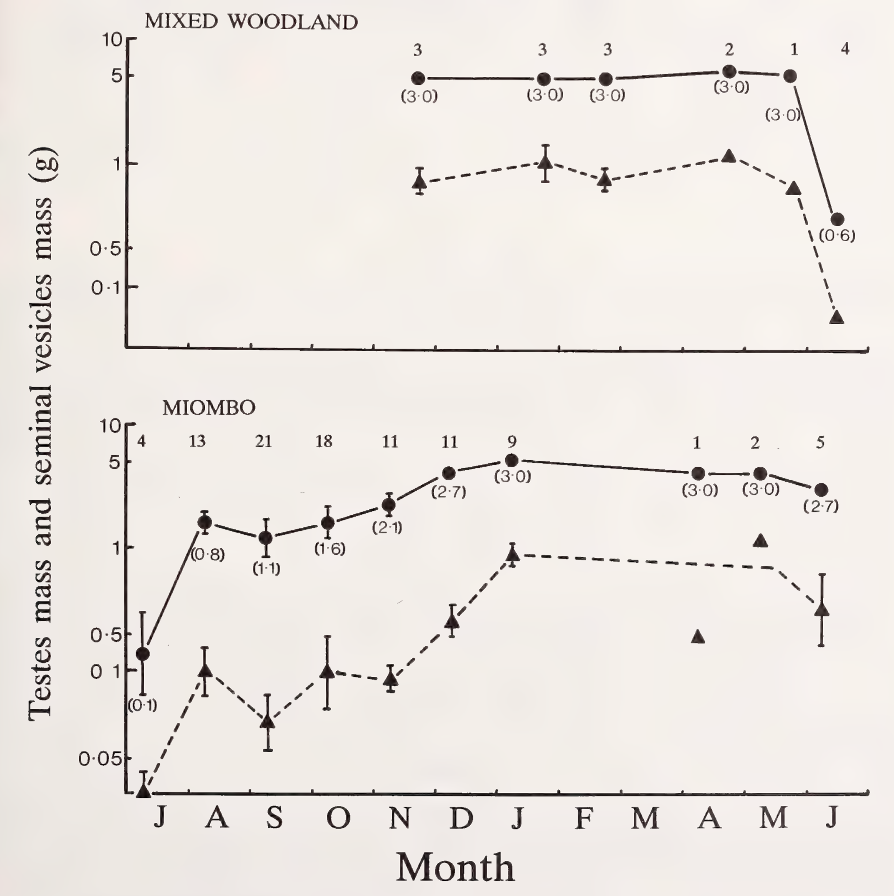


Fig. 3. Seasonal changes in testes mass (●—●) and seminal vesicles mass (▲----▲) of *T. leucogaster* in two habitats. Data points represent means and vertical lines ± 2 × S.E. Numbers in parentheses are the average sperm rating of the sample, and numbers above each figure represent sample sizes

regressed during the dry season (Fig. 3), but this regression was subject to considerable individual variation and individuals with large testes and fully mature sperm ratings were present throughout the year.

Litter size

The mean number of live embryos of 25 pregnancies in mixed woodland was 5.6 ± 0.29 (range 3–8) and of 10 pregnancies in Miombo was 4.8 ± 0.36 (range 3–6). In both areas, litter size increased as the breeding season progressed, from a mean of 4.2 during November and December to 6.5 during March and April in mixed woodland, and from 3 in December to 5 during March and April in Miombo. Both the difference between areas and the difference between months were significant when analyzed by two-way analysis of variance. Litter size was not significantly correlated with body mass or age.

Breeding rates and reproductive capacity

The potential annual production of young per adult female was calculated independently for each study area assuming a breeding period from September to April in mixed woodland and from December to April in Miombo. In mixed woodlands females could theoretically have had an average of five litters during the breeding season resulting in a production of 28 offspring, whereas females in Miombo could only have had an average of 2.5 litters resulting in 12 offspring during the breeding season.

Counts of placental scars indicated that no female had more than three litters and that it was unusual for females to have more than two litters. Thus, the high reproductive capacity in mixed woodland must have been achieved by a high turnover rate of adult females.

Population structure

The age structures indicated marked seasonal recruitment of young into the populations (Fig. 4). This was particularly evident in Miombo where most young were produced by females that had survived from the previous breeding season, although a few young matured rapidly and began breeding in April at the end of the breeding season. By the beginning of the dry season in May and June, most of the old animals had died off and been replaced by their offspring. In mixed woodland, the replacement of old animals by their offspring occurred in much the same way, but young began breeding by January and formed the majority of the breeding population by March. Thus, the Miombo population generally consisted of older individuals than the mixed woodland population except during the last three months of the study, and less of the Miombo young bred during the same breeding season of their birth compared to the mixed woodland population. Presumably these differences are mainly related to the length of the breeding season in the two areas.

Similarly, Chidumayo (1980) showed that the main recruitment of young occurred at the end of the rains and beginning of the dry season (March–June) in Zambia. These juveniles advanced in age and formed the majority of the population by the start of the following breeding season, after which they became rare or disappeared from the population.

Diet

The diets in the two study areas were superficially similar (Fig. 5). Seeds formed the bulk of the diet (50–75 %) throughout the year and insects were also commonly eaten (10–40 %). Only a small amount of stem and leaf material was consumed (< 10 %), and this was at a maximum during the rains and early part of the dry season. Towards the end of the rains and early part of the dry season (March–June) a small amount of fungi and lichens were also consumed. However, there was surprisingly little seasonal variation in diet (Fig. 5).

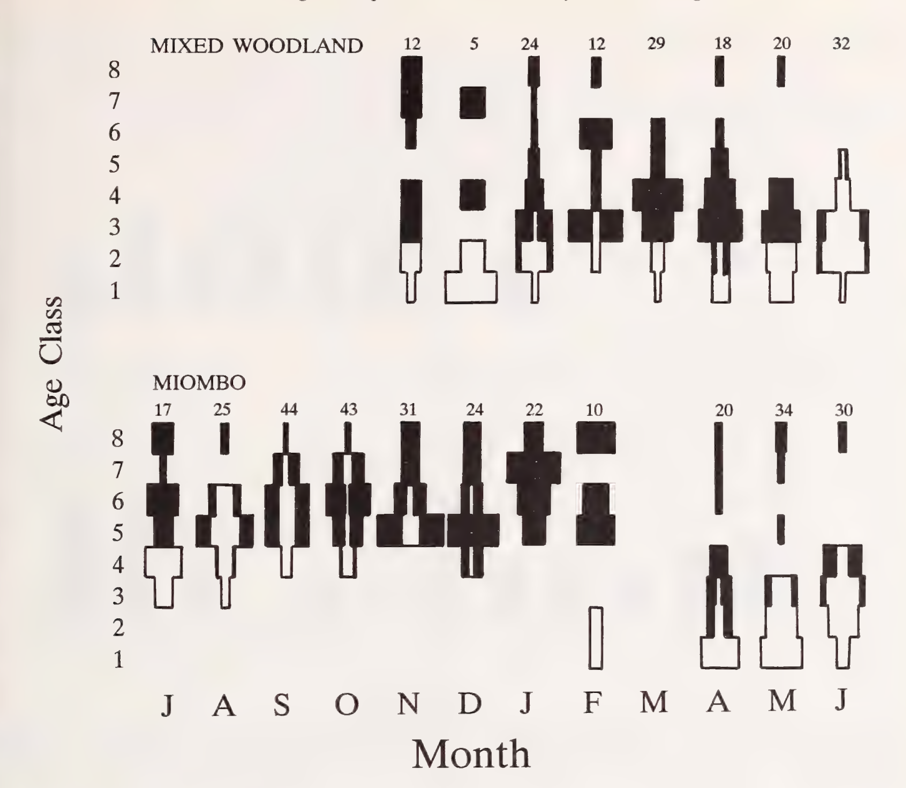


Fig. 4. Monthly age structure of *T. leucogaster* in two habitats. Open blocks represent immature animals and solid blocks represent mature animals. Sample sizes are shown above each figure

In contrast, Perrin and Swanepoel (1987) observed a marked seasonal variation in diet in the Transvaal: insects and seeds predominated during the rains and herbage was eaten in large amounts during the dry season. Overall, the diet consisted of 41.4 % insects, 32.2 % herbage, and 26.4 % seeds.

Discussion

Testes size and sex ratio

Information on adult male body mass, testes mass and adult sex ratios during the breeding season are summarized for different species of *Tatera* in the Table. There is a wide range of testes size in the genus, and the relative size of the testes of *T. leucogaster* is second only to *T. afra* which has the largest proportion of body mass allocated to testicular tissue that is known for any mammal (Kenagy and Trombulak 1986).

Testes size in mammals is considered to be related to copulatory frequency and consequently to the type of mating system (Harcourt et al. 1981; Kenagy and Trombulak 1986). There are two broad categories of mammalian mating systems: 1. Single-male systems, where a female mates with a single male, copulation is infrequent and the testes are small, and 2. multi-male systems, where a female mates with more than one male, copulatory frequency is high and the testes are large.

Little is known about the mating systems of most myomorph rodents although many are thought to be promiscuous, i.e. multi-male breeders (Kenagy and Trombulak 1986). Based on their study of the relationship between relative testes size and mating system, we

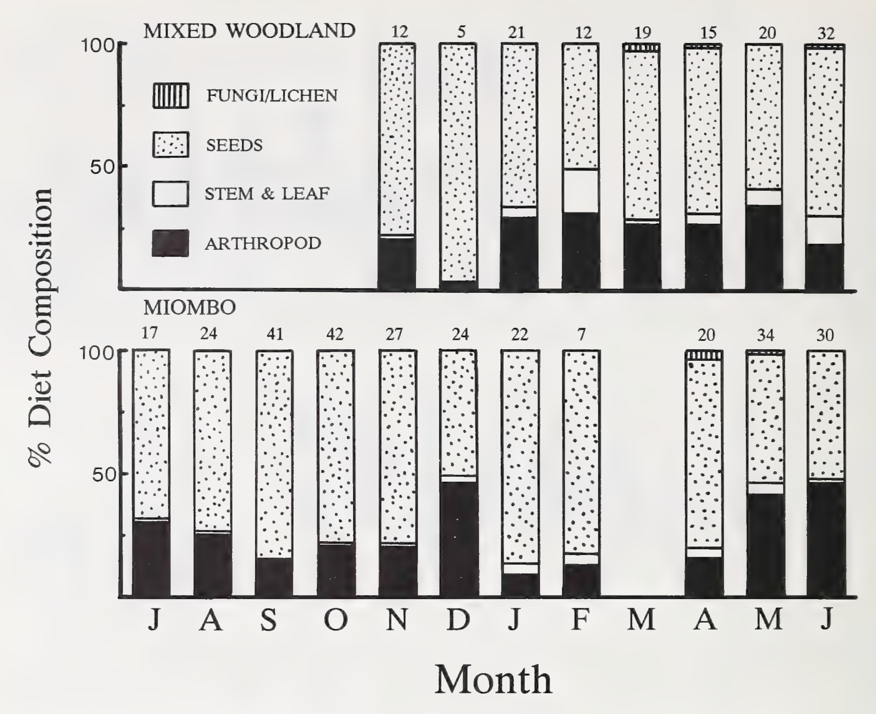


Fig. 5. Seasonal changes in diet composition of *T. leucogaster* in two habitats. Numbers represent sample sizes

would predict (Table) that *T. nigricauda* has a single-male breeding system and the other species have multi-male breeding systems. In this case we would expect *T. nigricauda* to be monogamous and have an even sex ratio (as observed) because the other type of single-male mating system, extreme polygyny in which a single male copulates with all females in a group, is not very likely in a small mammal with a dispersed distribution. The other species of *Tatera* probably have promiscuous mating systems with either even or skewed sex ratios. In fact there seems to be a relationship between adult sex ratios during the breeding season and relative testes size (Table). Species with small testes had even sex ratios and species with large testes had skewed sex ratios in favour of females.

The juvenile sex ratio of all species, except *T. brantsii,* were not significantly different from parity. Most juveniles matured between breeding seasons and so it is interesting to note that adult sex ratios outside of the breeding seasons were also not significantly different from parity. This implies that the change in sex ratio occurred at the time of breeding and so may be related to the type of mating system. The skewed sex ratios are probably the result of differential mortality rather than different capture rates because one would expect promiscuous males to be more active than females. In conclusion, it would seem that *Tatera* would make an interesting study animal for mammalian mating systems because of the wide range of testes size and adult sex ratios in different species of the genus.

The testes of *T. indica* (Prasad 1956), *T. leucogaster* (Perrin and Swanepoel 1987; this study) and *T. afra* (Allanson 1958) regress during the non-breeding season, whereas those of *T. nigricauda*, *T. robusta* and *T. valida* (Neal 1982) show little seasonal variation in size. *T. brantsii* breeds throughout the year (Allanson 1958). Thus, the regression of the testes shows a positive correlation with testes size (Table) in seasonally breeding *Tatera.*

Adult sex ratios and percentage of testes mass in relation to total body mass of adult males during the breeding season for different species of *Tatera*

Relative testes size is the ratio of observed mass to that predicted by the equation: Testes mass (g) = 0.031 × (Body mass g)$^{0.77}$ for rodents (Kenagy and Trombulak 1986). Sample size is for testes and body mass measurements

	Sample size (n)	Testes/Body mass (%)	Relative testes size	Sex ratio ♂♂/♀♀	χ^2 values	Reference
Tatera nigricauda	52	0.4	0.4	50/59	0.74	Neal 1982
T. robusta	5	2.2	2.1	5/8	0.69	Neal 1982
T. valida	23	2.9	2.8	22/23	0.02	Neal 1982
T. indica	35	2.7	2.9	80/76	0.10	Prasad 1956, 1961
T. brantsii	10	4.7	4.5	130/202	15.6***	Allanson 1958; Measroch 1954
T. leucogaster[1]	12	6.0	5.4	20/49	12.2***	This study
T. leucogaster[2]	13	6.2	5.5	22/41	5.7*	This study
T. afra	10	7.7	7.3	90/142	11.7***	Allanson 1958; Measroch 1954

[1] Mixed woodland area. – [2] Miombo area. * $p < 0.05$; *** $p < 0.001$.

Perhaps the regression of the testes is related to the energy costs of maintaining mature-sized gonads during the dry season when, presumably, food supplies are more limiting. The gonads and accessory reproductive glands of male *T. leucogaster* and *T. afra* comprise more than 10 percent of their body mass and so considerable savings of energy could be achieved by reducing the size of the reproductive system during the non-breeding season. There was considerable individual variation in the regression of the testes of *T. leucogaster* at Sengwa. During the dry season, the testes and seminal vesicles of animals provided with supplemental food were considerably larger than those of animals from non-supplemented areas (see Breeding Season below; Neal and Alibhai 1991), which suggests that the regression of the testes is related, at least in part, to energy consumption.

Breeding season

The population of *T. leucogaster* in mixed woodland appears to have started breeding in September 1987 approximately three months ahead of the Miombo population which began breeding in December 1987. This difference was not related to rainfall or temperature because these were similar in the two areas, which were only 8–9 km apart. The diets of animals from the two areas were also similar and were virtually identical in terms of the proportions of seeds, stem and leaf, and arthropods consumed in November (Fig. 5) when the mixed woodland population was breeding but the Miombo population was sexually quiescent.

There is circumstantial evidence, however, that food may be more abundant in the mixed woodland area compared to Miombo, which would allow a greater consumption of food and provide more energy for reproduction. First, a large proportion of Miombo is burnt annually at the start of the dry season whereas the mixed woodland area was never burnt. Such burns would decrease the abundance of seeds, which form a major component of the diet, and also of arthropods by reducing the plant biomass. Second, the density of small mammals in the mixed woodland (258 animals at 862 trap locations) was almost twice as high as that in Miombo (178 animals at 1029 trap locations) although the densities of *T. leucogaster* were similar in the two areas (123 *Tatera* at 862 trap locations in mixed woodland and 171 *Tatera* at 1029 trap locations in Miombo). Third, the larger body mass, litter size and reproductive rate of mixed woodland animals compared to Miombo animals

is also more consistent with the proposed availability of food in the two areas rather than other posible causes such as differences in population density or age structure. On the basis of age structure one would expect Miombo animals to be heavier on average than those in mixed woodland but the reverse was true; no relationship was observed between litter size and age; and the density of this species was similar in the two study areas. Finally, a reproductive response to extra food has been demonstrated for this species, at least for males (NEAL and ALIBHAI 1991). A field experiment in August 1987 provided supplementary seeds for a period of 10 d to a population in Miombo habitat. In seed supplemented areas both sexes were significantly heavier, the testes of the males were approximately twice as heavy, and the seminal vesicles were three to four times as heavy as those of animals from control (i.e. non-supplemented) areas.

Thus, the seasonal breeding cycle may be explained as follows. Animals cease breeding in May at the start of the cool dry season. This is probably a response to the rapid decline in minimum temperature (Fig. 1), when the animals are active, although a photoperiod response cannot be discounted. The cessation of breeding does not seem to be linked to the availability of food or moisture because both areas were still lush and green from the previous month's rain, and seeds and insects were plentiful. Breeding starts again at the beginning of the hot dry season in September if high quality food is sufficiently available, as would seem to be the case in the mixed woodland area. If food is insufficient, breeding is delayed until the onset of the rains when the availability first of insects, and then seeds, increases. This would explain the breeding delay in Miombo.

The general pattern of breeding of *T. leucogaster* in Zambia (CHIDUMAYO 1980) and the northern Transvaal (PERRIN and SWANEPOEL 1987) is similar to that described for the mixed woodland area in Sengwa. Food has been suggested to have an important influence on the reproductive cycle of this and other species of the genus (CHIDUMAYO 1980; NEAL 1982; PERRIN and SWANEPOEL 1987), and ROWE-ROWE and MEESTER (1982) have suggested that low temperatures can further influence the timing of reproduction of small mammals in South Africa.

Acknowledgements

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Zusammenfassung

Saisonale Schwankungen in der Fortpflanzung und in der Nahrungszusammensetzung beim Bushveld Gerbil Tatera leucogaster (Muridae: Rodentia) in Zimbabwe

Die Fortpflanzungsverhältnisse und die Nahrungszusammensetzung von *Tatera leucogaster* wurden in zwei Gebieten (in gemischtem Waldland und in Miombo) in der Sengwa Wildlife Research Region untersucht. In beiden Populationen fand während der kühlen Trockenzeit keine Fortpflanzung statt. Eine Population begann aber drei Monate vor der anderen sich fortzupflanzen. Die zwei Populationen zeigten ein ähnliches Nahrungsspektrum, und Regenfall und Temperatur waren in den untersuchten Gebieten ebenfalls ähnlich. Der Unterschied in der Fortpflanzungsdauer beider Populationen hing wahrscheinlich mit dem Nahrungsangebot zusammen.

In beiden Gebieten betrug das Gewicht der Testes der adulten Männchen etwa 6 % ihres Gesamt-Körpergewichts. Das Verhältnis von männlichen zu weiblichen adulten Tieren während der Fortpflanzungsperiode ergab mehr Weibchen.

Im gemischten Waldgebiet hatten die Weibchen eine durchschnittliche Wurfgröße von 5,6 ± 0,3. Daraus ergibt sich eine durchschnittliche jährliche Fortpflanzungskapazität von 28 Jungen pro adultem Weibchen. In Miombo hatten die Weibchen eine durchschnittliche Wurfgröße von 4,8 ± 0,4

und entsprechend eine geringere durchschnittliche jährliche Fortpflanzungskapazität von 12 Jungen pro adultem Weibchen.

Die Nahrung bestand hauptsächlich aus Samen (50–70 %) und Insekten (10–40 %) und in geringerem Maße aus Gräsern und Blättern (< 10 %). Es waren nur geringe jahreszeitliche Veränderungen im Nahrungsspektrum festzustellen.

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Habitat relations in *Ctenomys talarum* (Caviomorpha, Octodontidae) in a natural grassland

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Abstract

Tested the hypothesis that the spatial distribution of *Ctenomys talarum* ("tuco-tuco") in a natural grassland on a coastal cliff at Mar de Cobo, Argentina, is determined by topographic, soil and vegetation characteristics of the habitat.

In summer, there was no correlation between the number of "tuco-tucos" and any of the vegetation, soil or topography variables. In contrast, in autumn and winter, the number of animals was positively correlated with the density of grasses with small reserve organs (definite rhizomes). In spring, the number of animals was positively correlated with soil humidity, density and height of the vegetation, and density of grasses without reserve organs and with small reserve organs, and was negatively correlated with the sand percentage in the soil.

The results indicate that the spatial distribution of *Ctenomys talarum* is associated with the studied variables, although their relative importance varies seasonally.

Introduction

Rodents of the genus *Ctenomys* ("tuco-tucos") are subterranean and herbivorous. Populations are distributed throughout Argentina, southern Brazil, and parts of Paraguay, Bolivia, Uruguay, Perú and Chile (WOODS 1984). The "tuco-tucos" dig sinuous burrows with several openings that are plugged with vegetation and/or sand during the greatest part of the day and night. These burrows consist of a main gallery connected with shorter ones that end on or below the surface (CONTRERAS 1973; ALTUNA 1983).

Because movement underneath the earth is energetically very expensive, characteristics related to energetic balance and foraging costs are presumably under high selection pressure (VLECK 1981). Since the habitat productivity determines the foraging benefits and the soil hardness determines the costs, foraging economies should favor a maximum body size for each type of habitat such that benefits and costs are equal (VLECK 1981). The larger animals should occupy zones with high productivity and/or lighter soils. The subadults should occupy less favorable habitats, migrating to favorable zones when these are vacated because of the death of their previous occupants (PEARSON et al. 1968). Other habitats should be unsuitable because of excessive hardnesss of the soil or low food availability. Soil texture is also important in determining burrow temperature and ventilation, with sandy soils favoring gaseous exchange (MCNAB 1966; WILSON and KILGORE 1978). Consequently, factors such as topography and exposure of the occupied zones relative to dominant winds, and vegetation structure, should also affect *Ctenomys* habitat selection.

Because of the high energetic cost of digging, soil hardness could be the most limiting factor affecting the dispersion of subterranean rodents (BEST 1973; ABRAHAM 1980). Species with larger body size would be the most affected (BEST 1973; VLECK 1981). Along the Atlantic coast of Buenos Aires Province, Argentina, there is a clear halt of *Ctenomys* distribution between Santa Clara del Mar and Necochea (CONTRERAS and REIG 1965).

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CONTRERAS (1973) found a positive correlation between the textural type "sandy-clay-loam" of the second horizon and the presence of *Ctenomys*.

Tuco-tucos at Mar de Cobo (Partido de Mar Chiquita), where the habitat is heterogeneous, have a clumped distribution (BUSCH et al. 1989). The present study tests whether *Ctenomys* spatial distribution is associated with topography, soil and vegetation characteristics of the habitat; and evaluates their relative importance.

Study site

The experimental area covered a surface of 100 by 70 m divided in 10 by 10 m squares in Mar de Cobo (Partido Mar Chiquita, Buenos Aires Province, Argentina) on a coastal cliff where the vegetation was a natural grassland with predominance of species with rhizomes. To characterize the vegetation of the site, the frequency of occurrence of each species was calculated seasonally as the number of touches of green parts over the number of total touches. The dominant species in summer were *Panicum racemosum* (32 %), *Ambrosia tenuifolia* (17 %), and *Distichlis scoparia* (16 %). In autumn, *Panicum racemosum* (19 %), *Distichlis scoparia* (12 %), *Bromus unioloides* (8 %) and *Stipa neesiana* (7 %). In winter, *Bromus unioloides* (17 %), and *Stipa neesiana* (8 %); in this season, 61 % of the vegetation was dry, and warm season species such as *Panicum racemosum* and *Distichlis scoparia* dropped to 2 % and 4 % of green material, respectively. In spring, there were 19 % *Panicum racemosum*, 10 % *Bromus unioloides*, 10 % *Ambrosia tenuifolia*, 10 % *Distichlis scoparia*, and 8 % *Stipa neesiana*.

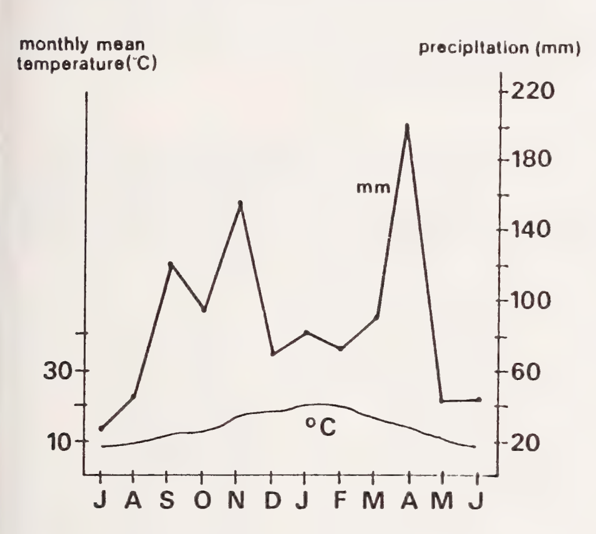


Fig. 1. Cilmatic data (1986). Source: Estación Aérea Mar del Plata. Data are plotted according to WALTER (1977)

In sixteen measurements, the sand percentage in the soil varied from 88 % to 99 %, winter soil moisture varied from 4 % to 19 %, spring soil moisture varied from 4 % to 15 %, and soil hardness varied from 7 to 52 $\vec{kg}/cm^2$. The topographic map showed that the difference in altitude between the lowest and the highest point of the study area was 2.4 m.

Fig. 1 shows climatic data for the year when the studies were conducted (1986). Data are plotted according to WALTER (1977).

Material and methods

The vegetation of the experimental area was sampled in March, May, August, and December 1986 by means of a non-destructive method which consisted of positioning a vertical needle and recording the canopy contacts (LEVY and MADDEN 1933; GREIG-SMITH 1964; HESLEHURST 1971; JONG et al. 1983). The needle was lowered systematically, each 20 cm, along four 70 m transects perpendicular to the coast. For each touch we recorded: the plant species, its height above the surface, and whether it was living. This method of sampling vegetation underestimates forbs and overestimates grass cover (GREIG-SMITH 1964), and may explain the low percentages of *Hydrocotyle bonariensis,* which never exceeded 5 % in the plots.

Samples of soil were collected at a depth of 20 cm in August and December along the same transects used to study vegetation. Four 500 g samples were obtained systematically in each transect. Organic matter from soil samples was removed using hydrogen peroxide. Sand percentages were determined by leaching the silt and clay fractions. These latter percentages were determined only in the winter samples, because they do not vary throughout the year. Soil moisture was determined by

differential weight readings before and after drying the soil samples at 105 °C. Soil hardness was measured along the transects with a soil penetrometer.

The contours of the topographic map were traced with respect to the highest point that was set at the arbitrary value of zero. The greater values are the lower points of the study site.

Density and spatial distribution of *Ctenomys* were obtained in a simultaneous study in the same grid (Busch et al. 1989) by capture-recapture methods. Population size on the grid was estimated as the minimum number known alive between trapping intervals (Petrusewicz 1983). The Jolly-Seber method (Caughley 1977) was also used to estimate population size, but in the present study we used the former situation (Fig. 2), and data on their spatial distribution to estimate the number of animals in each square of the grid. Poisson distribution analysis indicated that the distribution of animals on the study area was clumped (df. = 69; P = 0.01).

The following variables were measured for each square in each season:

a. Vegetation: Total cover (total number of touches); Green cover (number of touces of green parts); Mean maximum height (cm); Cover of grasses with large reserve organs (indefinite rhizomes); Cover of grasses with small reserve organs (definite rhizomes); Cover of grasses without reserve organs; Cover of forbs with reserve organs (rhizomes); Cover of forbs without reserve organs (Table). We grouped the vegetation this way because we considered that the presence of rhizomes is an important character in *Ctenomys* nourishment.
b. Soil: Percentage sand; Relative humidity; Soil hardness ($\overrightarrow{kg}/cm^2$).
c. Relief: Distance from the coast (m); Relative elevation (m).
d. *Ctenomys talarum:* Number of individuals.

Vegetation, soil and relief data were analyzed complementing ordination and classification techniques. Principal Components Analysis (PCA) (Harris 1975) and Cluster Analysis (CA) by the nearest neighbor with simple linkage (Orlóci 1978) using 1-Pearson correlation coefficient for sample distances, were performed. Simple correlations were established between sample positions along the first seven axes and sample animal numbers. SYSTAT statistical program was used.

Vegetation groups and their principal species

Grasses with large reserve organs	Grasses with small reserve organs	Grasses without reserve organs
Panicum racemosum	*Festuca arundinacea*	*Bromus unioloides*
Distichlis scoparia	*Poa bonariensis*	*Stipa neesiana*
Paspalum vaginatum	*Poa lanigera*	*Dactylis glomerata*
Stenotaphrum sp.	*Paspalum dilatatum*	*Phalaris platensis*
Cynodon dactylon	*Setaria geniculata*	*Lolium multiflorum*
		Lolium perenne
		Hordeum leporinum
		Sporobolus indicus
Forbs with reserve organs	**Forbs without reserve organs**	
Ambrosia tenuifolia	*Medicago lupulina*	
Hydrocotyle bonariensis	*Melilotus officinalis*	
Solidago chilensis	*Phyla cannescens*	
Oxalis cordobensis	*Stellaria media*	
	Anagallis arvensis	
	Sonchus oleraceus	
	Geranium dissectum	
	Rapistrum rugosum	
	Brassica campestris	
	Dichondra repens	
	Gamochaeta spicata	

Results

Fig. 3 shows data ordination, grouped according to CA. The figure is a bidimensional representation of the first two spring axes. Although analysis of all the seasons were performed and plotted, spring results are the most interesting since animal spatial distribu-

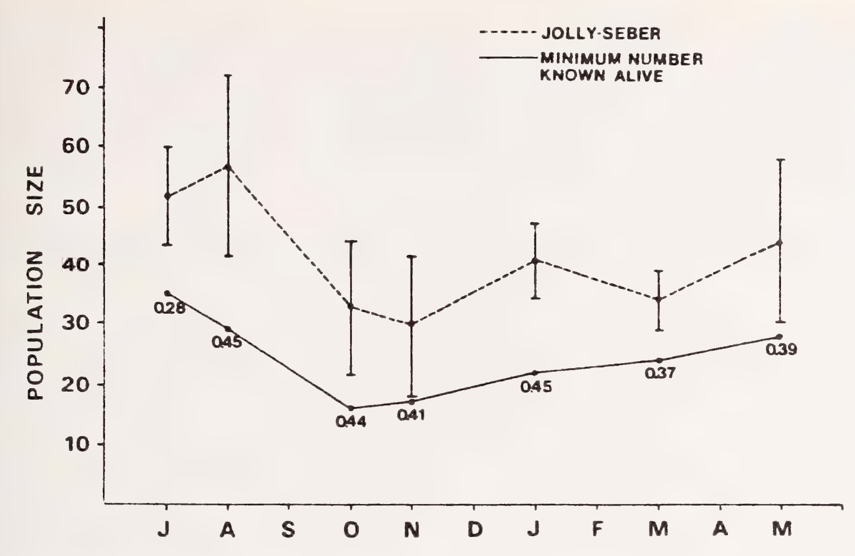
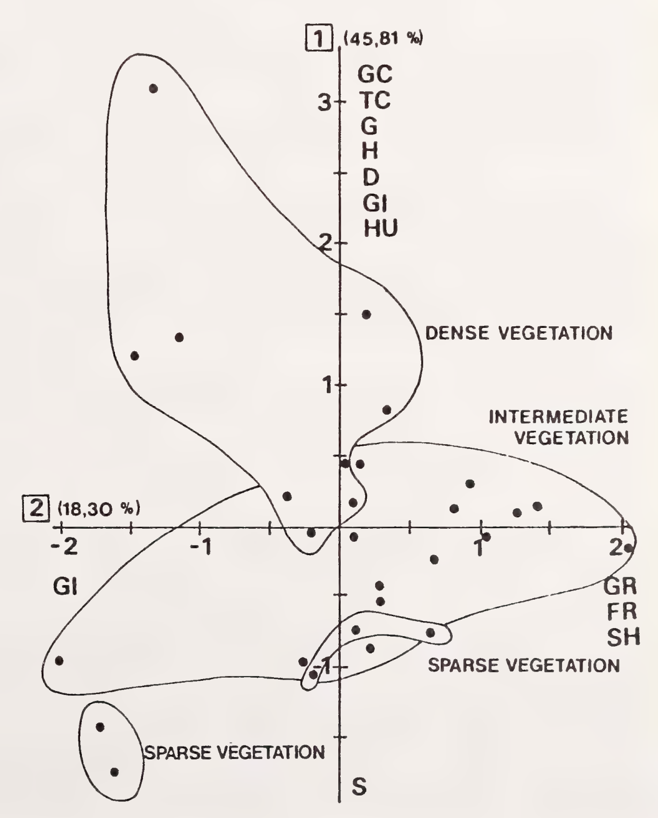
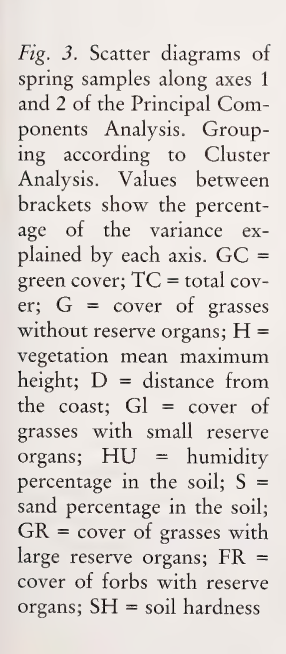


Fig. 2. Estimates of number of *Ctenomys talarum* on a 100 by 70 m grid in Mar de Cobo, Argentina, July 1985–May 1986. Vertical lines indicate 2 SE above and below the Jolly Seber estimate. Numbers indicate proportion of males in the sample. (Taken from Busch et al. 1989)




Fig. 3. Scatter diagrams of spring samples along axes 1 and 2 of the Principal Components Analysis. Grouping according to Cluster Analysis. Values between brackets show the percentage of the variance explained by each axis. GC = green cover; TC = total cover; G = cover of grasses without reserve organs; H = vegetation mean maximum height; D = distance from the coast; Gl = cover of grasses with small reserve organs; HU = humidity percentage in the soil; S = sand percentage in the soil; GR = cover of grasses with large reserve organs; FR = cover of forbs with reserve organs; SH = soil hardness

tion is closely related to vegetation heterogeneity at the community level. In the other seasons, animal distribution is associated with intracommunity heterogeneity (fine grain), and thus, scatter diagrams are poorly informative. A common aspect of the analyzed seasons is that the principal tendency of data variability (ax 1 of the PCA) shows a contrast between samples with sparse vegetation and sandy soil, and samples with dense and high vegetation and humid soil, more distant from the sea. Such contrast always explains over 38 % of the total variance.

In March (summer) no correlation was found between the number of "tuco-tucos" and the position of the samples along the first seven axes. In this season, no soil samples were collected; as a consequence, there were no moisture data.

In May (autumn), the number of animals was significantly correlated ($P < 0.05$) with the position of the samples along ax 3 of the PCA, and significantly correlated ($P < 0.055$) with the position of samples along ax 4. No correlation was found with any of the other first seven axes. Ax 3 opposes forbs without reserve organs and grasses that have small reserve organs, with grasses and forbs that have large reserve organs. The loading of these variables in ax 3 is 0.730, 0.474, 0.679 and 0.439 respectively, being animal distribution positively correlated with the first two variables. Ax 3 explains 13.45 % of the total variance. Ax 4 shows a gradient of samples with and without grasses that have small reserve organs. The loading of this variable in ax 4 is 0.601, being the number of animals positively correlated with the presence of grasses that have small reserve organs. Ax 4 explains 8.07 % of the total variance. In this season, no soil samples were collected.

In August (winter), the number of "tuco-tucos" was significantly correlated ($P < 0.05$) with the position of samples along ax 4. No correlation was found with any of the other first seven axes. Ax 4 shows a gradient of samples with and without grasses that have small reserve organs. The loading of this variable in ax 4 is 0.793, being the number of animals positively correlated with the presence of grasses that have short reserve organs. Ax 4 explains 9.80 % of the total variance.

In December (spring), the number of animals was significantly correlated ($P < 0.05$) with the position of the samples along axes 1 and 6. No correlation was found with any of the other first seven axes. Ax 1 opposes samples of sandy soils (loading 0.826) and low vegetation cover, with samples of high vegetation cover (total cover, green cover, cover of grasses with small reserve organs and without reserve organs, height of the vegetation, whose loadings lie between 0.768 and 0.949), humid soils (loading 0.675), more distant from the sea (loading 0.794). The number of animals is positively correlated with high vegetation cover and humid soils. Ax 1 explains 45.81 % of the total variance (Fig. 3). Ax 6, which only explains 3.53 % of the total variance, shows a gradient of samples with and without forbs that have reserve organs (loading 0.418), being the number of animals positively correlated with the samples without forbs that have reserve organs.

Discussion

Soil texture and humidity are important factors in the distribution of subterranean rodents. Abraham (1980) found that *Ctenomys talarum* does not build its burrows in soils containing 25 % or more of clay; Hansen and Beck (1968) found that when the soil moisture exceeds 50 %, pocket gophers *(Thomomys talpoides)* move to dryer sites.

The percentage of sand in the soil of our experimental area is high, never below 87 %, therefore, texture and hardness should not be limiting factors in the dispersion and occupation of new zones of the area. As sand percentage is very high, soil humidity is low, even in the colder seasons. Soil humidity and probably soil temperature, conditioned by the vegetation cover, can be very important when climatic factors are extreme. The fact that the number of animals in late spring (Fig. 3) was positively correlated with humidity,

suggests that low soil humidity and high soil temperature can affect the occupation of certain areas during the hot season. Therefore, in warm months, favorable zones should be those of higher humidity, and consequently less sandy and with greater density and height of the vegetation (Fig. 3). Also, in spring, most of the vegetation is green, so that the positive correlation of the "tuco-tucos" with the density of the vegetation can have a dietary explanation. Results of this kind would be expected in summer. In this season, on the contrary, no correlation was found between animal density and any of the variables examined. During this season, green vegetation (warm season species) is ubiquitous. Also, this period coincides with the end of the breeding season and the dispersion of the subadults who will occupy the less favorable areas (PEARSON et al. 1968). In this situation, the animal distribution could be mainly determined by social factors.

When the aerial productivity of the vegetation is low in autumn and winter, the animals' energetic requirements are higher because of the regulation of body temperature and the lactation of the young. The breeding season lasts nine months, from the end of May to the end of February with a peak in August (BUSCH et al. 1989). The autumn (ax 3 and 4 of the principal components analysis) and winter (ax 4) association of animal density with grasses that have small reserve organs, suggests a relationship between energetic requirements and animal spatial distribution. Most of this vegetation is composed of cool season species, and is therefore green when most of the other vegetation is dry. Further, REIG (1970) and LOHFELDT et al. (1989), suggest that *Ctenomys* eats much more aerial than underground vegetation.

Also, in autumn, the positive correlation of animals with the presence of forbs without reserve organs (ax 3 of the PCA), can be explained by animal continuous earth movements that favor the implantation of annual forbs.

Although the tendency of the variable along the axes is subtle, the negative correlation of animal spatial distribution with the presence of forbs that have reserve organs in autumn (ax 3 of the PCA) and spring (ax 6), suggests a rejection of these species, which are principally *Ambrosia tenuifolia* and *Hydrocotyle bonariensis*. This rejection can have a dietary explanation, since LOHFELDT et al. (1989) suggest that *Ctenomys talarum* prefers grasses in autumn and spring.

In conclusion, the clumped distribution of *Ctenomys talarum* in the area, can be correlated with environmental factors, the presence of grasses with small reserve organs being the most important determinant in autumn and in winter, and soil humidity, density and height of the vegetation in spring. Also, data suggest that other factors, like animal behavior, may be important determinants of animal spatial distribution during certain seasons.

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Zusammenfassung

Habitat-Beziehungen von Ctenomys talarum (Caviomorpha, Octodontidae) auf natürlichem Grasland

Auf einer bestimmten Fläche von natürlichem Grasland an der Küste von Argentinien nahe Mar de Cobo, Provinz Buenos Aires, wurde untersucht, in welcher Weise die räumliche Verteilung von Individuen der Art *Ctenomys talarum* (Tukotuko) durch Topographie, Bodenbeschaffenheit und Vegetation bestimmt ist. Für den Sommer ergab sich keine Korrelation von Individuenanzahl zu irgendeinem der untersuchten Faktoren. Im Herbst und Winter war demgegenüber die Anzahl der

Tiere positiv korreliert mit der Dichte von Gräsern, die mit kleinen Speicherorganen ausgestattet sind. Auch für den Frühling ergab sich eine positive Korrelation, diesmal jedoch mit der Bodenfeuchtigkeit, mit Dichte und Höhe der Vegetation, sowie mit der Dichte von Gräsern sowohl ohne besondere, als auch mit kleinen Speicherorganen. Andererseits wurde eine negative Korrelation zum prozentualen Sandanteil des Bodens festgestellt. Die Ergebnisse deuten an, daß die räumliche Verteilung von Tukotukos zu den untersuchten Faktoren in Beziehung steht, im Laufe des Jahres jedoch in unterschiedlicher Weise.

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WISSENSCHAFTLICHE KURZMITTEILUNGEN

Use of an active badger sett by Egyptian mongooses, *Herpestes ichneumon*, in Southwest Spain

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Badgers *(Meles meles)* use dens dug by themselves for rest and protection (Kruuk 1978; Neal 1986). Badgers' setts are often used as a refuge by other mammals, including several carnivores (Neal 1986). Some of the carnivores use deserted setts (see Neal 1986, for a review). Small carnivores also use active setts, although only casually, whilst foxes *(Vulpes vulpes)* use them more regularly and even for breeding in. Here I report for the first time deserted badger setts being used by Egyptian mongooses *(Herpestes ichneumon)* and describe in detail the regular use of an active sett by several radio-tracked mongooses in Doñana National Park, SW Spain, from September 1987 to March 1989.

Mongooses in this area are typically diurnal and usually use burrows at various locations to rest in at night and for resting periods of several hours during the day (Delibes and Beltrán 1985; Palomares 1986). During the two years of study at least nine mongooses have used badger setts as a resting area and overnight refuge. In some situations the density of the vegetation made it difficult to establish the type of burrow used. Four deserted badger setts which displayed two to five entrance holes were used by seven mongooses (3 males and 4 females). One active sett was used by 4 males and 4 females as follows (between the parentheses the tracking day number is shown): males: HM1, at least 3 times (117); HM2, 2 times (205); HM3, 1 time (24); HM7, 26 times (53); females: HH4, 2 times (38); HH6, 1 time (163); HH10, 30 times (154); HH12, 19 times (103). Three individuals, HH10, HH12 and HM7 were also located in the sett during the daytime, both resting and active. Of the mongooses captured whose home range included the sett, only one was never recorded inside it.

The above mentioned badger sett, in the bank of a small stream, is dug out of earth and covers an area of approximately 400 m^2. Eleven entrances are visible, although there appear to be more between the vegetation below which the sett is found. Of these 11 only 6 showed signs of use in March 1989. From earlier visits, no important changes in the entrances in active use were observed. Throughout the study the sett was in daily use by badgers as confirmed by their tracks, and it can be considered the principal sett of a badger clan (Kruuk 1978). Usually the mongooses used 3 entrances for arrival and departure, whilst the badgers used only 2; one of them being utilised by both species. The resting site of two of the marked mongooses, HH10 and HM7, was located very close to the entrances most frequently used by the badgers. Different behaviour is usually observed with foxes, since they tend to use the parts of the sett the badgers do not (Neal 1986). Wijngaarden and Peppel (1964) have speculated that the use of badger setts by foxes is due to the absence of optimal refuge sites. For mongooses, which frequently use the abundant rabbit warrens of Doñana, this is not the case.

In the study area, badgers and mongooses display different activity patterns. The

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mongoose is diurnal (Delibes and Beltrán 1985; Palomares 1986), the badger nocturnal. Despite this difference, both species overlap underground for four to ten hours a day.

The appreciable size difference between the two species in Doñana (approximately 7–9 kg for badgers compared to 3 kg for mongooses) makes such great mutual tolerance unexpected, since confrontations are known to be frequent between other carnivores (e.g. Rogers and Mech 1981). However, badgers, which are very aggressive among themselves (Kruuk 1978), generally show little interspecific aggression (Neal 1986). Moreover, there appears to be no disadvantage for the mongoose, in spite of the fact that the two species have a certain similarity of diet and therefore possibly compete for resources in the area (Martin-Franquelo and Delibes 1985; Palomares 1986).

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Fully formed first lower premolars in a White-tailed deer (*Odocoileus virginianus Zimmermann*, 1780)

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The first artiodactyls (e.g. *Diacodexis*) from the lower Eocene of North America, Europe and Asia, had a full dentition (I 3/3, C I/I, P 4/4, M 3/3), without diastema (Carroll 1988). The first ruminants (e.g. *Archaeomeryx*) from the upper Eocene of Asia had already lost P^1, were on the way to losing their upper incisors, and P_1 was caniniform and located in a short diastema separating P_2 from the lower canine (Viret 1961). Then in the lower Miocene, from *Blastomeryx* onwards, P_2 had disappeared almost completely being seen in only a few specimens of *Blastomeryx* itself, then not at all afterwards (Matthew 1908; Frick 1937). Ever since that time, i.e. for the last 20 million years, most artiodactyls (i.e. the bovids and cervids) have had a tooth formula reduced to I 0/3, C 0/1, P 3/3, M 3/3, with a long diastema between P_2 and the incisiform lower canine.

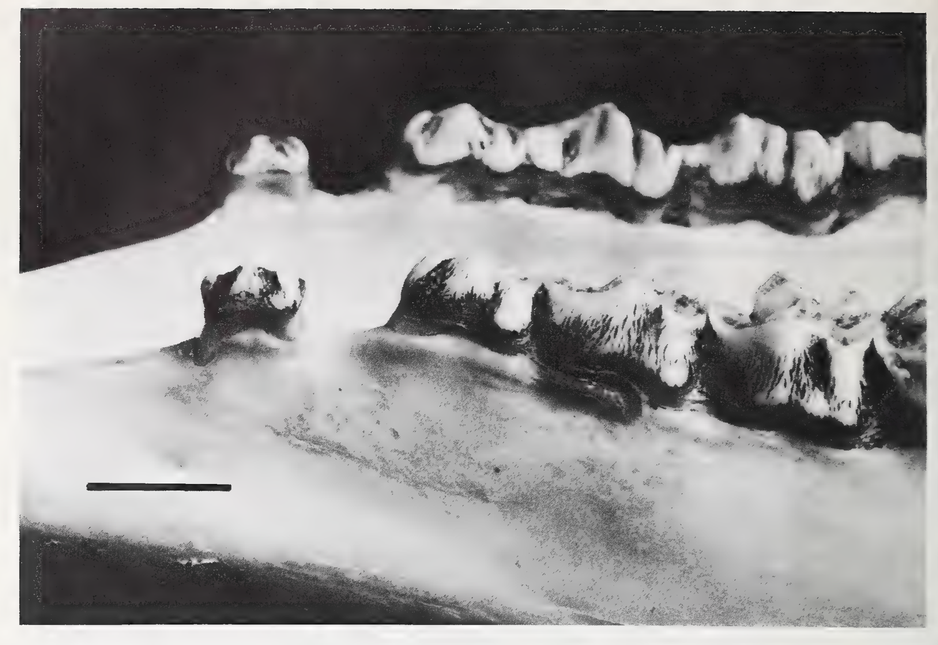
Even though this has been the condition for about 20 million generations, one occasionnally sees one of the long lost tooth being expressed in the phenotype of a present-day artiodactyl. This is the case for P_1 for instance that has been reported for some nine species of bovids and cervids (*Gazella thomasii:* Robinette and Archer 1971; *Sylvicapra grimmia:* Child and Riney 1964; *Bison bison:* Fuller 1954; *Capra pyrenaica:* Vigal and Machordom 1987; *Odocoileus virginianus:* Mech et al. 1970; *O. hemionus:* Robinette et al. 1977; *Rangifer tarandus:* Banfield 1961; Miller and Tessier 1971; *Cervus elaphus canadensis:* Moran and Fairbanks 1966; and *Capreolus capreolus:* Bubenik and Wurtzinger 1967; Meyer 1985). From 15 studies that have reported on supernumerary teeth in bovids and cervids (including the ones listed above), I could compute that the overall frequency of occurence of P_1 in the two families is less (and sometimes considerably less) than one in 3000 individuals.

The case described here is a young adult male *O. virginianus,* hit by a car north of Montréal (45° 45′ N, 74° 45′ W) during the winter 1988. The animal was healthy, weighing 78.5 kg, and having a total length of 181 cm. Its skull has a condylobasal length of 289 mm and a bizygomatic width of 116 mm. Its upper tooth row measures 74 mm while the lower (excluding P_1) is 81.1 mm long.

This case is particularly interesting not only because of its rarity, but because both its permanent P_1 are very similar to what those teeth looked like in pre-cervid artiodactyls. In most of the cases reported above the first premolars are small, peg-like, single rooted, and sometimes limited to one side, i.e. it is not only a vestigial tooth but a rather stunted form of it. On the contrary, the P_1 of the specimen presented here, are symmetrical in size, shape, and placement, have two fully formed roots (both measure 7.4 mm long on the left P_1 that came loose after the drying of the jaw), and have the size and shape that one would predict by extrapolating the trend seen from P_4 to P_2 in any normal white-tailed deer (Fig.). The length and height of the crown of the P_1 are 6.7 and 3.7 mm on the right side, and 7.3 and 3.5 mm on the left. Finally, each P_1 has three cusps in a straight line (Fig.).

On both sides P_1 is separated from P_2 by 6.5 mm, a placement very similar to the one seen in some modern suids like *Sus scrofa,* one of the few present artiodactyls that have

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Vestigial P_1 in an adult male white-tailed deer seen from the left side. The black bar is 10 mm long

retained their P_1. The diastema separating P_2 from the lower canine is 78.5 mm long, 96.8 % of the length of the lower tooth row (excluding P_1). That is about the same value as in white-tailed deer without P_1 (mean ± S.D. for 5 males and 5 females = 94.3 ± 5,3 %). Thus P_1 has not caused a lengthening of the diastema, it merely occupies a short segment of it. The form of the P_1 of this white-tailed deer is premolar-like. They are not the caniniform P_1 seen in living camelids or suids, in *Archeomeryx,* or in the Oligocene *Hypertragulus* (Carroll 1988; Viret 1961).

A specimen such as the one described here lends concrete support, from a contemporary animal, to Riney's (1951) proposal to consider the first premolar present in a deer jaw as being P_2. It is also a stricking case of genetic atavism. It is however unclear whether the genes responsible for the production of P_1 are present in only a few contemporary deer, or else are present in all, but are being repressed in some way. Finally, the present case gives us a chance to examine, in a fresh specimen, what the dentition was presumably like millions of years ago.

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Chromosomes of the Argentine Andean mouse, *Akodon andinus* (Cricetidae: Sigmodontinae)

By Maria Beatriz Espinosa, A. D. Vitullo and Maria S. Merani

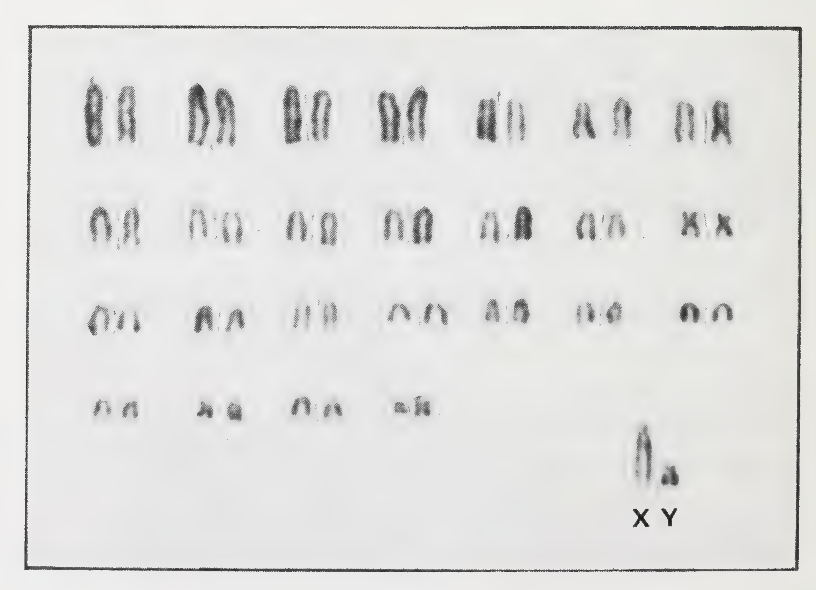
Centro de Investigaciones en Reproducción, Facultad de Medicina, Universidad de Buenos Aires, Buenos Aires, Argentina

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Cytogenetic analysis was performed on six specimens of *A. andinus* (Philippi, 1858) (two males and four females) collected at Plaza de Mulas, in the eastern slope of the Aconcagua, province of Mendoza, Argentina, at 4,200 m above sea level. Specimens were identified as *A. andinus* by external and cranial characteristics by Prof. Julio Contreras, and deposited at the Systematic Collection of the CECOAL, province of Corrientes, Argentina. Chromosomes were obtained from bone marrow by routine methods, and Giemsa-Stained G-banded according to Seabright (1971).

All specimens studied showed a 2n = 52 (NF = 60) karyotype with three distinctive pairs of medium- and small-sized metacentric autosomes, and 22 pairs of telocentrics decreasing gradually in size (see Fig.). Besides minimal variations in positioning of metacentric autosomes, this karyotype is similar both in diploid number, chromosomal morphology and lengths to those previously reported for *A. xanthorhinus, A. olivaceus, A. longipilis* (Rodriguez et al. 1983), and *A. illuteus* (Liascovich et al. 1989).

G-banded chromosomes were arm-to-arm compared with a banded karyotype of *A. olivaceus* (kindly provided by Dr. L. Vidal-Rioja from the Instituto Multidisciplinario de Biologia Celular, La Plata, Argentina), showing entire similarity between banding patterns



Giemsa-stained karyotype of *Akodon andinus;* 2n = 52, NF = 60

of both species. Similarly, whole G-band identity has also been reported for *A. xanthorhinus, A. olivaceus,* and *A. longipilis* from Chile (RODRIGUEZ et al. 1983), and *A. illuteus* and *A. longipilis* from Argentina (LIASCOVICH et al. 1989). These results strongly support the contention that speciation in the southern lineage of *Akodon* proceeded without chromosomal change from a generalized 2n = 52 karyotype, which likely is the primitive condition for *Akodon* (REIG 1987). Although banding patterns had not been reported, the same 2n = 52 karyotype has been described for *A. sanborni* and *A. jelski,* and the related genera *Chelemys* and *Geoxus* (PEARSON 1984).

We thank Dr. A. CASTRO-VÁZQUEZ for providing the animals employed in this study, Prof. J. CONTRERAS for the identification of specimens, and Dr. L. VIDAL-RIOJA for providing us with original pictures of G-banded karyotypes of *A. olivaceus.* Thanks also to Dr. E. ROLDÁN, for his comments and improving of the English.

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POLLAK, G. D.; CASSEDAY, J. H.: **The Neural Basis of Echolocation in Bats.** Zoophysiology, Vol. 25. Ed. by W. BURGGREN, S. ISHII, H. LANGER, G. NEUWEILER, D. J. RANDALL. Berlin-Heidelberg-New York-London-Paris-Tokyo-Hong Kong: Springer Verlag 1989. 143 pp., 82 figs. DM 128,–. ISBN 3-540-50520-2

This monograph reviews the physiology of the auditory system in bats, from periphery to midbrain. The authors focus on recent neuroanatomical and electrophysiological investigations in the horseshoe bats *(Rhinolophus)* and the mustache bats *(Pteronotus)*; comparisons between these constant-frequency bats and frequency-modulated species are somewhat rare.

The first chapter gives an introduction to echolocation by characterizing the different types of ultrasonic calls and their use in various orientation situations. The main parts deal with different aspects of the major auditory nuclei of the bats' brainstem, the cochlear nucleus, olivary complex, lateral lemniscus and inferior colliculus. It is shown that the principal characteristic of the system is a tonotopic organization, remapping the frequency arrangement of the cochlea in the nuclei of the auditory system. Intensively described are the monaural and binaural pathways, emanating from the anteroventral cochlear nucleus. These parallel pathways extract different information from the acoustical signal and converge at the inferior colliculus. A great number of investigations deal with the physiological properties of auditory neurons. The characteristic neurons of the different nuclei are considered. For instance the E-I units (excited by the contralateral, inhibited by the ipsilateral ear) in the lateral superior olive and the colliculus inferior, that are sensitive to interaural intensity disparities. It is shown that these neurons play a crucial role for the localization of sounds at different azimuthal positions. Equally important are "constant latency neurons" that encode range information.

This volume is written with great scientific competence, and gives an excellent insight in the neural processes associated with hearing in bats. Due to the instructive introductions, the complex subjects of the different chapters are easy to understand, even for the interested reader who is not professionally involved in neurophysiology. U. SCHMIDT, Bonn

HEIDECKE, D.; STUBBE, M.: **Populationsökologie von Fledermausarten.** Teil I u. II. Kongreß- und Tagungsberichte der Martin-Luther-Universität Halle-Wittenberg, WB 1989/20 (P36); 368 S. August-Bebel-Str. 13, O-4010 Halle-Saale. ISBN 3-86010-194-3

Dieses ist der Referateband der 4. DDR-Tagung zur Fledermausforschung vom 11.–13. 11. 1988 in Meisdorf, Kreis Aschersleben. Veranstalter waren die Sektion Biowissenschaften der Martin-Luther-Universität in Halle-Wittenberg, die Biologische Gesellschaft der DDR (hier die AG-Fledermausforschung) sowie das Institut für Landschaftsforschung und Naturschutz in Halle. Die beiden Bände enthalten insgesamt 33 Referate und sind dem großen Fledermausforscher JOHANN CHRISTIAN DANIEL SCHREBER (250. Geburtstag) gewidmet. Einleitend wird die Bedeutung von Halle für die klassische Fledermausforschung vom 18. bis zum 20. Jahrhundert dargestellt (Biographischer Anhang). Eine Gruppe von Vorträgen befaßt sich mit dem Status der Fledermausarten in den verschiedenen Bezirken der DDR. Berichtet wird ferner über die Situation einzelner Arten, über Arealgrenzen, Erstnachweise und über besondere Wochenstuben. In 8 Referaten wird der Einsatz von Fledermauskästen behandelt (Arbeitsmethoden). Den Abschluß bilden Vorträge über die Echoortung (Einsatz von Bat-Detektoren). Beide Bände geben einen guten Überblick über den gegenwärtigen Stand der Fledermausforschung in der DDR. E. KULZER, Tübingen

KLÖTZLI, F.: **Ökosysteme: Aufbau, Funktionen, Störungen.** 2., völlig überarb. Aufl. Stuttgart, New York: Gustav Fischer Verlag 1989. UTB Nr. 1479. 464 S., 166 Abb., 87 Tab. DM 44,80. ISBN 3-437-20403-3

Die 1. Auflage erschien 1980 unter dem Titel „Unsere Umwelt und wir". Wie schon aus dem Literaturverzeichnis zu ersehen, das etwa zur Hälfte nach 1979 erschienene Zitate enthält, ist die jetzt vorliegende Fassung nicht nur im Titel verändert, sondern auch erheblich umgestaltet. Das Buch ist in vier Abschnitten gegliedert: Struktur, Kreisläufe, organismische Beziehungen und menschliche Einflüsse. Im Vordergrund stehen weniger Ökosysteme (= Biozönosen + Biotope) als vom Menschen ausgehende Umweltgefahren, die mit vielen Zahlen in Tabellen und Diagrammen untermauert werden. So erfährt man eine Menge zu den Themen saurer Regen, Ozonschild, Treibhauseffekt, Müllentsorgung und Recycling, Schwermetalle, Herbizide und Radionuclide in der Natur, Ausbreitung von Wüsten oder Nutzungsänderung in der Landwirtschaft. Zu diesen Fragen dürfte das Buch auch wertvoll und wichtig sein. Leider gilt das weniger für zoologische Aspekte. So werden bei den

guten, alten Klimaregeln inter- und intraspezifische geographische Variabilität vermischt, Rehe sollen in den Polargebieten wesentlich größer sein als in südlicheren Breiten. (Wo kommen sie in den Polargebieten vor? Skandinavische Rehe sind nicht größer als mitteleuropäische.) Unter den Beispielen für konvergente Tierformen findet man „eurasisches Steppenmurmeltier und Präriehund" oder „Oppossum/Ratte" (S. 7). Nach S. 22 mußten beim Übergang aufs Land Lungen und Nieren entwickelt werden. Tabelle 115 zeigt die Beziehungen zwischen Lemming-Häufigkeit und Wollgras-Dichte nach Tast und Kalela (nicht Kalena). Die Unterschrift behauptet, die Arbeit sei 1971 durchgeführt worden, sie bezieht sich aber, wie die zugehörige Graphik ergibt, auf den Zeitraum von 1962–1970. Die Ordinate gibt nicht die in 100 Nächten in Fallen gefangenen Lemminge, sondern die Fangzahlen bei 100 Fallennächten wieder.

Mit der Definition von Fitneß als „die Fähigkeit auch unter ungünstigen Bedingungen Nachkommen zu erzeugen" kann man ebenso wenig einverstanden sein wie mit RNS „als wichtiger Transfer- oder Botensubstanz für organische Stoffe (z. B. Eiweiße)". Unter der „Erklärung der Fachausdrücke" findet man eine ganze Reihe weiterer zumindest sehr mißverständlicher Formulierungen bei ATP, Aminosäuren, Chromosom, Assimilation, organische Substanz, Parasit, Polypeptid, Sukzession, Tritium, Wirkungsgrad. Auf Seite 93 liest man, daß Wasser „mit Säuren und Basen gepufferte Lösungen" bildet. Auf Seite 239 regt Streß die Nebennierenrinde zu vermehrter Adrenalinausschüttung an. Bei den in Tab. 45 aufgeführten Nahrungsketten handelt es sich um Beispiele aus Nordamerika, bei denen es oft schwer fällt, die betreffende Art zu identifizieren, weil nur deutsche Trivialnamen vorkommen. Eine Nahrungskette „Tanne–Reh–Wolf" (S. 225) dürfte es kaum geben. In der Nahrungspyramide Abb. 108 findet man als Zusatz zur Stufe der „Ruderfußkrebschen": z. B. B. Krill, *Euphausia superba*". Auf Seite 217 wird *Stellaria media* als Sternmiere bezeichnet. Selbst bei dem Schachspiel stimmt etwas nicht, wenn Patt als Situation erklärt wird, „wo beide Könige auf ihrem Feld festsitzen und sich gegenseitig blockieren". Die Quellen der Abbildungen sind zwar genannt, aber nicht im Literaturverzeichnis zitiert.

Die zahlreichen Lapsus machen mißtrauisch hinsichtlich der Richtigkeit sonstiger Angaben. Deshalb kann das in Druck und bildlicher Gestaltung (abgesehen von den oft zu kleinen Fotos) sehr ansprechende Buch leider nur mit erheblichen Bedenken empfohlen werden als ein Werk, dessen Aussagen man sich nicht ungeprüft zu eigen machen darf. J. Niethammer, Bonn

Eisenberg, J. F.: **Mammals of the Neotropics.** Vol. I: The Northern Neotropics. Panama, Columbia, Venezuela, Guyana, Suriname, French, Guiana. Chicago, London: University Chicago Press 1989. 449 pp., num. illustr., 21 colour plates, num. tables. Cloth US $ 97.75 (ISBN: 0-226-19539-2); paper US $ 40.45 (ISBN: 0-226-19540-6)

Based on his own extensive fieldwork in South and Central America, the well-known North American mammalogist John F. Eisenberg has published a remarkable book, which will certainly become a MUST on the bookshelves of people interested in neotropical mammals.

After a short introduction to historical biogeography and contemporary habitats of the northern part of South America, the author deals with the order Marsupialia and 12 eutherian orders that live in the above-mentioned part of the continent. It is very helpful that the author organizes the text according to a strict format. The orders are presented by giving a diagnosis, a short summary on their geographical distribution, followed by a brief account on palaeontological history and on classification. Each family that belongs to one of the mammalian orders living in the northern neotropics is introduced by an account on taxonomy, a diagnosis, the discription of its geographical distribution and a summary on its natural history. The different species belonging to the families are described; essential measurements are given in these descriptions and colours as well as other physical characteristics are summarized. A clear description of the range and habitat of the respective species is given and a standardized map shows its distribution. An account of the natural history concludes the section on each species. At the end of each chapter on a mammalian order, a modern, useful and truely international list of references is supplied.

The text of this most noteworthy book is concluded by two interesting chapters. One deals with speciation and faunal affinities of mammals in the northern neotropics, the other with mammalian community ecology. As islands are useful indicators of speciation rates, Eisenberg discusses the mammals of Trinidad, Tobago, Isla Margarita, Grenada, and three of the Netherland Antilles. According to the author little specific distinctiveness has evolved on the above-mentioned islands, but sub-specific differences can be noted.

To conclude, an index of scientific and one of common names helps the reader to make full and easy use of the materials compiled in this volume.

The referee is certain that this book, and, most probably, also the forthcoming companion, will soon become most useful sources of reference, not only for scientists working on that continent, but also for those interested in general zoogeography, ecology or taxonomy. Researchers might wish to apply the remarkable wealth of data that was made available by John F. Eisenberg for comparative studies or for specialized investigations in neotropical mammals. P. Langer, Gießen

Subscription information for USA, Canada and Mexiko obtainable from Paul Parey Scientific Publishers/IR Unltd., 35 West 38th Street, Suite 3 W, New York, NY 10018, USA.

Erscheinungsweise und Bezugspreis 1991: 6 Hefte bilden einen Band. Jahresabonnement Inland: 338,– DM zuzüglich 13,80 DM Versandkosten, Gesamtpreis 351,80 DM einschließlich 7 % Mehrwertsteuer. Jahresabonnement Ausland: 338,– DM zuzüglich 18,– DM Versandkosten. Das Abonnement wird zum Jahresanfang berechnet und zur Zahlung fällig. Es verlängert sich stillschweigend, wenn nicht spätestens am 15. November eine Abbestellung im Verlag vorliegt. Die Zeitschrift kann bei jeder Buchhandlung oder bei der Verlagsbuchhandlung Paul Parey, Spitalerstraße 12, W-2000 Hamburg 1, Bundesrepublik Deutschland, bestellt werden. Die Mitglieder der „Deutschen Gesellschaft für Säugetierkunde" erhalten die Zeitschrift unberechnet im Rahmen des Mitgliedsbeitrages.

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Die Zeitschrift für Säugetierkunde veröffentlicht Originalarbeiten und wissenschaftliche Kurzmitteilungen aus dem Gesamtgebiet der Säugetierkunde, Besprechungen der wichtigsten internationalen Literatur sowie die Bekanntmachungen der Deutschen Gesellschaft für Säugetierkunde. Verantwortlicher Schriftleiter im Sinne des Hamburgischen Pressegesetzes ist Prof. Dr. Dieter Kruska.

Zusätzlich erscheint einmal im Jahr ein Heft mit den Abstracts der Vorträge, die auf der jeweiligen Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde gehalten werden. Sie werden als Supplement dem betreffenden Jahrgang der Zeitschrift zugeordnet. Verantwortlich für ihren Inhalt sind ausschließlich die Autoren der Abstracts.

Manuskripte: Manuskriptsendungen sind zu richten an die Schriftleitung, z. Hd. Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Biologie-Zentrum, Neue Universität, Olshausenstr. 40–60, W-2300 Kiel, Bundesrepublik Deutschland. Für die Publikation vorgesehene Manuskripte sollen gemäß den „Redaktionellen Richtlinien" abgefaßt werden. In ihnen finden sich weitere Hinweise zur Annahme von Manuskripten, Bedingungen für die Veröffentlichung und die Drucklegung, ferner Richtlinien für die Abfassung eines Abstracts und eine Korrekturzeichentabelle. Die Richtlinien sind auf Anfrage bei der Schriftleitung und dem Verlag erhältlich.

Sonderdrucke: Anstelle einer Unkostenvergütung erhalten die Verfasser von Originalbeiträgen und Wissenschaftlichen Kurzmitteilungen 50 unberechnete Sonderdrucke. Mehrbedarf steht gegen Berechnung zur Verfügung, jedoch muß die Bestellung spätestens mit der Rücksendung der Korrekturfahnen erfolgen.

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Excavation of three badger (*Meles meles* L.) setts

By T. J. Roper, A. I. Tait, S. F. Christian and D. Fee

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Abstract

Excavated and described three badger setts in the south of England. Two of the setts were classified as subsidiary setts and the third as an annex. Each consisted of a main network of interconnected tunnels associated, in two of the setts, with 2–3 small separate burrows. Total tunnel lengths were 28, 30 and 53 m respectively and estimated total volumes of the setts were 1.1, 1.1 and 2.1 m^3. No sett exceeded a depth of more than 1 m and mean depths of the tunnel systems were 61, 56 and 52 cm respectively. All three setts contained bedding material (dry grass) but only one (the annex) contained enlarged chambers, faeces and badger bones.

Introduction

One of the most striking features of the European badger is its habit of constructing complex underground burrows or "setts". Within the confines of their setts badgers sleep, breed, overwinter and take refuge when alarmed; and in addition the sett forms a focus for social interactions between the different members of a badger group (Neal 1977; Kruuk 1989). Although a few setts have been accurately described and mapped (Likhachev 1956; Jensen 1959; Cowlin 1967; Frewin 1976; Leeson and Mills 1977; Roper et al. 1991) we still know comparatively little about the structure or internal environment of setts; and little serious thought has been given to the question of why badgers need elaborate setts in the first place (for a recent review see Neal and Roper 1991).

In the present study we describe three setts that were about to be destroyed by a road development. Prior to excavating the setts in question an attempt was made to determine whether or not they belonged to separate social groups and whether they should be classified as main setts, subsidiary setts, annexes or outliers (Kruuk 1978; Bock 1986; Thornton 1988).

Material and methods

Study area

The excavated setts were located in open farmland immediately to the north-west of Brighton, about 3.5 km inland from the south coast of England. The landscape consisted of a range of rounded chalk hills (the South Downs) containing patches of permanent pasture and scrub (mainly hawthorn *Crataegus monogyna*, elder *Sambucus nigra*, blackthorn *Prunus spinosa* and brambles *Rubus* spp.) in between larger areas of arable planting (mostly of wheat *Triticum aestivum*).

Location of setts

A survey carried out in April 1989 revealed six setts falling into two separate spatial groups, one of four sets and the other of two (see Fig. 1). Of the group of four setts, sett 1 was by far the largest, having 9 entrances of which 7 showed clear signs of use. Setts 2 and 3, by comparison, had only 3 and 4 entrances respectively at the time of the survey, while sett 4 had a single entrance; and none of these setts appeared heavily used. Given their close proximity to one another it seemed likely that all four setts were within the territory of a single social group, and this was subsequently confirmed when the territory boundaries were mapped using the technique of bait-marking (Kruuk 1978).

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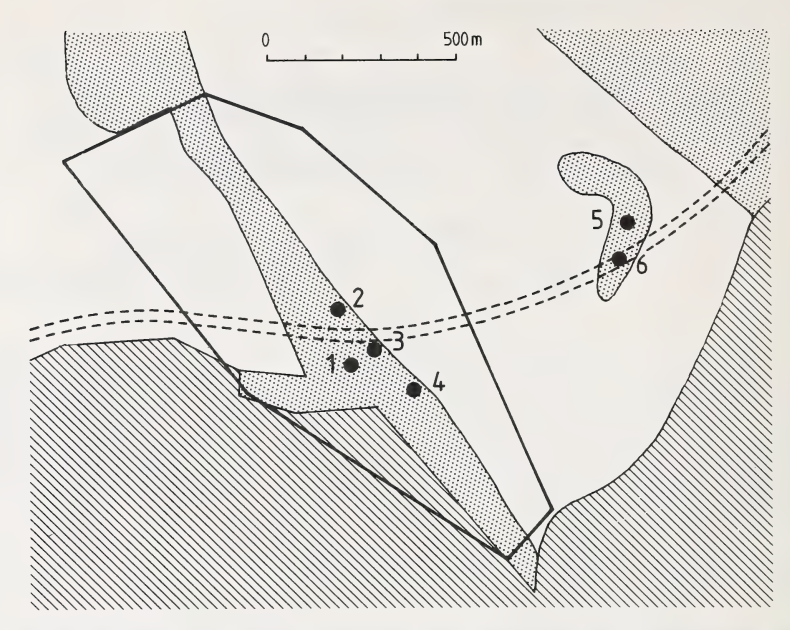


Fig. 1. Map of the study area showing position of setts (numbered 1–6). Dotted areas: grassland. Hatched areas: housing. Open areas: arable fields. Solid line: estimated territory boundary surrounding setts 1–4. Double broken line: route of new road

Of the pair of setts in the second group, sett 5 had 11 entrances of which 7 showed clear signs of use, while sett 6 had 5 entrances of which 4 showed clear signs of use. The two setts were connected by a well-worn path and although the territory boundaries surrounding the setts were not determined, it was clear from the proximity of the setts and their interconnectedness that both belonged to a single social group.

Of the six setts identified in Fig. 1 only setts 2, 3 and 6 were excavated since the remaining setts were not threatened by the new road. Setts 2 and 3 were located on a north-east facing slope, sett 2 at the top of the slope (altitude 95 m) and sett 3 near the bottom (altitude 80 m). Sett 2 was surrounded by dense scrub containing occasional mature sycamore trees *(Acer pseudoplatanus)*, while sett 3 was in open grassland dotted with occasional hawthorn trees *(Crataegus monogyna)*. Sett 6 was located on a west-facing slope at an altitude of 102 m in open grassland dotted with hawthorn trees. In all three cases the soil consisted of an open sandy loam to a depth of about 1.5 m, over chalk subsoil.

Method of excavation

The excavations were carried out in April 1990. Several months prior to this (in October 1989) all three setts were fenced off with one-way gates to exclude badgers from them (for a description of the method see Harris et al. 1988). When it was clear that the setts were no longer occupied the fences were removed and excavation was immediately begun.

The excavation itself was carried out with a small mechanical digger (Kibota KH20) or by hand when features such as tunnel intersections and nest chambers were encountered. Sett entrances were first identified with numbered surveyor's poles and plotted on a scale map. A 1.5 m-deep trench was then dug across one end of the sett, 2 m beyond the furthest entrance. The wall of the trench nearest the sett was gradually dug away, thus moving the trench progressively through the sett and exposing the underground tunnel system. As excavation proceeded tunnels and chambers were measured and plotted on a scale map, and the depth of the floor of each tunnel relative to the soil surface was measured to the nearest 10 cm, at intervals of approximately 2 m.

The length of each sett was measured as the furthest distance between any two extremities of the tunnel system. Sett width was measured orthogonal to the line joining these two points. Sett volume was calculated from the dimensions of tunnels and chambers, using the formulae of Leeson and Mills (1977).

Table. **Dimensions and contents of the three excavated setts**

Sett No.	Length (m)	Width (m)	Estimated volume (m^3)	Total tunnel length (m)	Mean tunnel depth (cm)	Entrances	Chambers	Bedding	Latrines	Badger remains
2	18	6	1.1	28	61	8	0	1	0	0
3	8	7	1.1	30	56	7	0	2	0	0
6	21	8	2.1	53	52	10	3	4	0	1

Results

The Table summarises the dimensions and contents of the three setts and Fig. 2 shows a plan view of each sett.

Sett 2

This consisted of four separate burrow systems, with tunnels totalling 28 m in length. Three of the burrows consisted of simple shallow tunnels only a few metres long, with single entrances, all of which were disused. The fourth system was larger and more complex, consisting of an interconnected network of tunnels radiating off from a central entrance, with four additional entrances around its outer limits. Two of the latter entrances were disused.

No obvious chambers were found, though tunnels tended to widen out where they intersected. Nor was there any evidence of badger faeces or badger remains (bones, teeth etc). A small amount of bedding material was found at one point in the main tunnel system, consisting of dry grass (about 1 litre) together with several chocolate wrappers and potato-crisp packets. Several of the tunnels had been extended by rabbits and at one point the excavation disclosed a rabbit nest containing four juveniles.

Sett 3

Sett 3 consisted of a single burrow system totalling 30 m in length, with four open entrances and three disused entrances. The system was essentially two-dimensional, with almost all tunnels running at a depth of 55–65 cm below the soil surface. The general plan of the system was of a single central tunnel forming the long axis of the sett, off which ran, more or less orthogonally, a number of separate tunnels.

The sett contained no enlarged internal chambers but a small amount of nest material (about 1 litre of dry grass) was found at two points where intersecting tunnels widened out. There were no badger faeces or other remains.

Sett 6

This sett consisted of three separate burrow systems: a single short burrow, 1.5 m long, with one entrance; a W-shaped burrow, 10.5 m long, with two entrances; and a larger interconnected network of tunnels, totalling 41 m in length, with five open and two blocked entrances. The two small burrows were separated from the large one by a distance of 8 m. Tunnel depths varied from 30–80 cm.

The large burrow system contained four distinct chambers which were the shape of a squashed sphere, 60–70 cm in diameter and 40–50 cm in height, with bowl-shaped floors. From their shape and symmetry, and the smoothness of their

walls, these were easily distinguished from other places, such as intersections, where the tunnel system widened out. One chamber was empty; the others contained small amounts of dry grass. In addition bedding material (dry grass) was found in one of the tunnels. A single deposit of faeces was found near one of the chambers containing bedding.

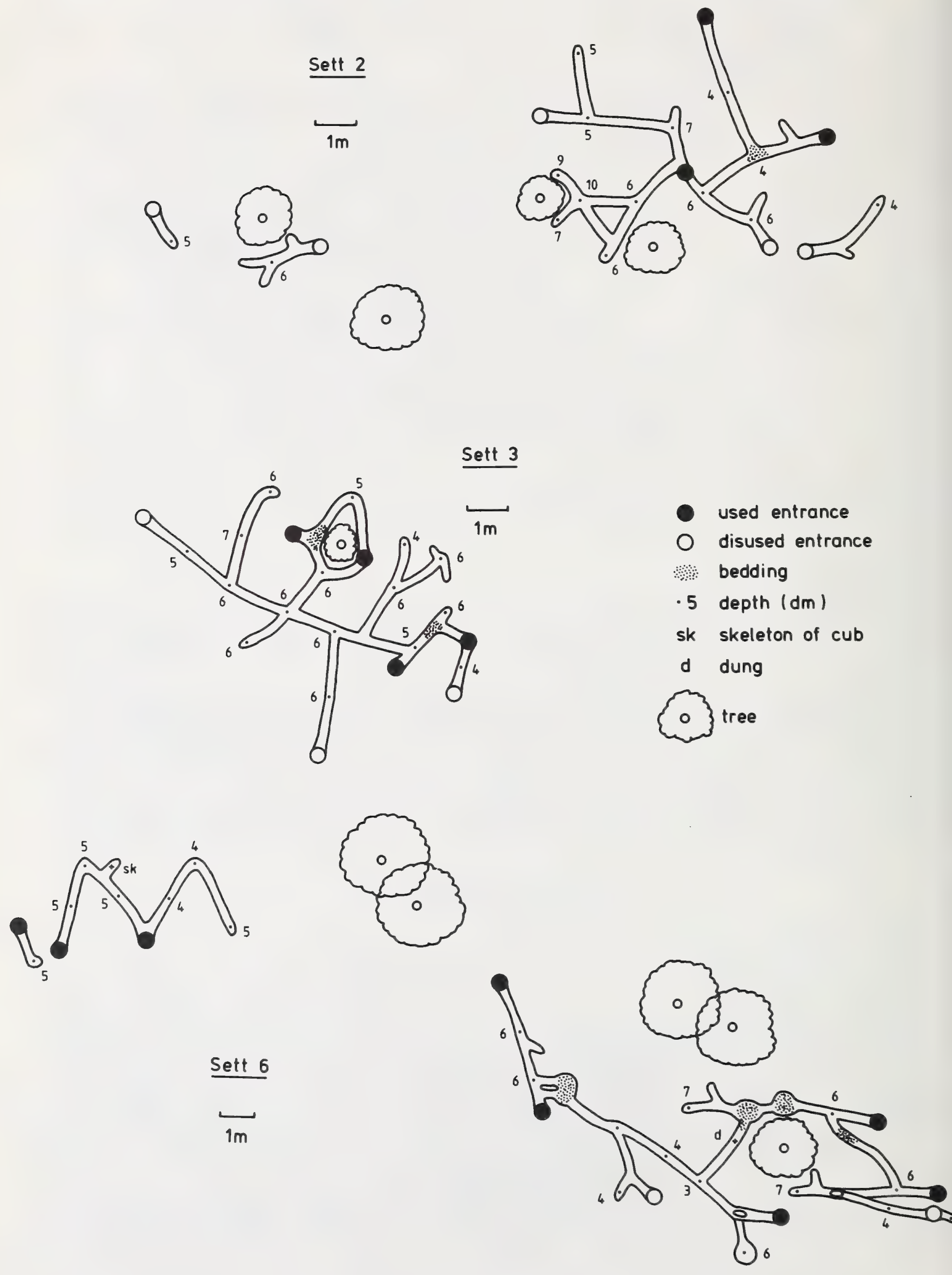


Fig. 2. Plan of setts 2, 3 und 6

No badger remains were found in the large system, but the skeleton of a cub was recovered from the small W-shaped burrow.

Discussion

A comparison of the architecture of the three setts reveals some striking similarities but also a number of differences. As regards the similarities, all three setts had tunnels of about the same size and shape (ie, about 25 cm wide × 15 cm high, with an arched roof and flattened floor), running at about the same average depth (50–60 cm). All three setts were essentially two-dimensional: only at two points in sett 6 did tunnels join in the vertical plane. All three setts had multiple entrances, some of which were disused; all three contained at least one nest of dry grass; and all three showed signs of occupation by rabbits as well as badgers. On the other hand, sett 3 consisted of a single burrow system whereas setts 2 and 6 also included two or three small separate burrows; and setts 3 and 6 each had a clear longitudinal axis running orthogonal to the slope into which they were dug, whereas sett 2 was roughly circular in plan. Furthermore, only sett 6 contained enlarged chambers, faeces and badger bones.

In explaining these similarities and differences at least three factors are relevant. First, certain features of badger setts, most notably their two-dimensional character and the size and shape of tunnels and chambers, show little variation from sett to sett (compare the present results with those of Likhachev 1956; Jensen 1959; Cowlin 1967; Frewin 1976; Leeson and Mills 1977; Roper et al. 1991). These sett characteristics may result from stereotyped, species-typical aspects of badger digging behaviour. Second, some features of setts, such as their size, complexity and depth depend at least in part on the nature of the soil in which they are dug (Bock 1988; Neal and Roper 1991). That these features were similar in the three setts described here would not then be surprising, given that all three were constructed in similar soil.

Third, there seems little doubt that badgers dig different types of sett for different purposes. Thornton (1988) distinguishes four types of sett: main setts, annexes, subsidiary setts and outliers. A "main sett" is a permanently occupied sett with many entrances and large spoil heaps; an "annex" also has many entrances but is not permanently occupied and is within 150 m of a main sett, to which it is connected by a well-used path; a "subsidiary sett" has fewer entrances, is not always occupied and is not obviously connected with a main sett; and an "outlier" has only one or two entrances and is only occasionally occupied. (See also Likhachev 1956; Neal 1977; Kruuk 1978 for similar attempts to classify setts in terms of size and use.) Applying these criteria to our three setts, we conclude that setts 2 and 3 were subsidiary setts. Thus, they were within the territory of an obvious main sett (sett 1, see Fig. 1), both had several entrances, but neither was regularly occupied. Sett 6, by contrast, seems to have been an annex: it was close to a larger main sett (sett 5), was linked to this main sett by an obvious path and was continuously in use in the year prior to excavation.

While it is agreed that main setts form the permanent home of a social group and are used for breeding and overwintering, the functional significance of annexes and subsidiary setts is less clear. Of our three setts only the annex contained nest chambers and latrines, suggesting that annexes may be better fitted for permanent or semi-permanent occupation (see also Roper et al. 1991). In addition the annex contained the skeleton of a cub. These observations are consistent with the idea that annexes are used for breeding by subordinate members of a social group, who may risk being attacked by a dominant animal if they remain within the main sett (Neal 1977).

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Zusammenfassung

Die Struktur dreier Baue des Dachses (Meles meles L.)

In den South Downs nordwestlich von Brighton in Südengland wurden drei Dachsbaue ausgegraben, vermessen und kartiert. Alle drei Baue bestanden aus einem Netz von Röhren, die bis 80 cm tief unter der Erdoberfläche verliefen. Alle enthielten trockenes Gras, aber nur in einem Bau fanden sich ein Kessel, Kot und Knochen eines Dachses, eines Jungtiers. Die Tunnellängen betrugen 28, 30 und 53 m, die Volumina der Baue 1.1, 1.1 und 2.1 m^3, die Zahl der Eingänge war 3, 4 und 5.

Offenbar war keiner der Baue ein Hauptbau. Vielmehr war der größte von ihnen offenbar ein auch als Wurfbau genutzter Nebenbau, die beiden übrigen waren separate Ergänzungsbaue.

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A study of allozyme evolution in African mongooses (Viverridae: Herpestinae)

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Abstract

Using horizontal starch gel electrophoresis, allozyme variation at 18 protein loci was investigated in 48 specimens representing seven species of mongooses (Viverridae: Herpestinae: *Cynictis penicillata, Helogale parvula, Suricata suricatta, Atilax paludinosus, Herpestes ichneumon, Galerella sanguinea* and *G. pulverulenta*) and one species of genet (Viverridae: Viverrinae: *Genetta tigrina*). Fourteen loci were polymorphic, and ten of these varied between species. Phenetic analysis of genetic distances (Nei 1978) suggested a relatively recent and "explosive" radiation of the extant Viverridae. Cladistic analyses (taking as outgroup the genet *Genetta tigrina*), involving distance Wagner trees from genetic distances (Rogers 1972), and parsimony analysis of ordered, multistate locus characters, produced congruent trees which suggested an early origin of *Atilax*, followed by a trichotomous split involving: 1. *Galerella*, 2. *Herpestes* and 3. a "social" lineage, comprising *Helogale, Suricata* and *Cynictis*. Aspects of the molecular phylogeny were supported by palaeontological, morphological, karyological and behavioral evidence. Owing to unequal rates of change in different lineages, phenetic and cladistic analyses of the allozyme data produced discordant trees, and the cladistic approach is to be preferred for analysing phylogenetic relationships among the mongooses.

Introduction

Relationships among the mongooses (Viverridae: Herpestinae) are poorly understood (Wozencraft 1989a). Several, largely conflicting, phylogenetic schemes have been proposed for the mongooses, based on independent studies involving morphological (Gregory and Hellman 1939; Petter 1969; Baker 1987), palaeontological (Hendey 1974), karyological (Fredga 1972) and behavioral (Baker 1987) evidence. Furthermore, a lack of consensus is evident in certain aspects of mongoose classification, such as the status of *Galerella* [subgenus of *Herpestes* (Wozencraft 1989b) or a full genus (Meester et al. 1986)], and the recognition of the mongooses as a separate family (Wozencraft 1989b) or as a subfamily of Viverridae (Rosevear 1974; Meester et al. 1986). Taxonomic instability also exists concerning the numbers of species that should be recognised in certain genera such as *Galerella* (sensu Meester et al. 1986), *Helogale, Bdeogale*, and *Crossarchus* (see Rosevear 1974; Honacki et al. 1982; Goldman 1984; Meester et al. 1986; Watson and Dippenaar 1987; Wozencraft 1989b).

Molecular techniques, including allozyme electrophoresis, have proved to be useful in resolving evolutionary and taxonomic relationships in the carnivoran families Felidae, Canidae and Ursidae (for a review see Wayne et al. 1989). The aim of the present study was to analyse allozyme variation in seven species of Southern African mongooses and one species of genet *Genetta tigrina*, in an attempt to resolve evolutionary and taxonomic relationships in the carnivoran family Viverridae (Herpestinae). Allozyme data were analysed as genetic distances and as qualitative characters, using both phenetic and cladistic (parsimony) approaches.

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Material and methods

Tissues (liver, kidney, heart and/or muscle) were collected from 48 specimens representing seven species of Southern African mongooses and one species of genet *Genetta tigrina* and these were stored in liquid nitrogen prior to electrophoretic analysis. Viverrid specimens were collected by live-trapping, shooting and by retrieving tissues from previously frozen carcasses obtained from fresh road kills. In the latter case most carcasses were donated by the Natal Parks Board. In three specimens, carcasses had been de-gutted and only muscle (or muscle and kidney) tissue could be obtained. Of the total sample of specimens collected, 35 specimens, representing eight populations of the yellow mongoose *Cynictis penicillata*, have been previously analysed for within-species allozyme variation at 28 loci (TAYLOR et al. 1991).

Details of specimens, methods of collection and sample sizes are given in Table 1. Voucher specimens were deposited in the Durban Natural Science Museum, the MacGregor Museum, Kimberley, the National Museum, Bloemfontein, and the Transvaal Museum, Pretoria.

The present study is based on starch (SIGMA: 12.5 %) gel electrophoretic results from 18 genetic loci encoding the following 15 proteins and enzymes (electrophoretic procedures, which are taken mainly from SELANDER et al. 1971; SHAW and PRASAD 1969; HARRIS and HOPKINSON 1976; and RICHARDSON et al. 1986, are described in detail in TAYLOR et al. 1990): albumin (ALB), catalase (CAT), glucose dehydrogenase (GDH), glutamate-oxaloacetate transaminase (GOT), glycerol dehydrogenase (GCDH), glycerol-3-phosphate dehydrogenase (GPD), haemoglobin (HB), isocitrate dehydrogenase (IDH), lactate dehydrogenase (LDH), malate dehydrogenase (MDH), malic enzyme (ME), phosphogluconate dehydrogenase (PGD), glucosephosphate isomerase (PGI), phosphoglucomutase (PGM), superoxide dismutase (SOD). Haemoglobin was present in sufficient quantities in blood associated with the tissue homogenates to permit its resolution in the present study. Optimum resolution of haemoglobin was obtained using a discontinuous buffer system (in this case, the lithium hydroxide-tris citrate buffer of SELANDER et al. 1971). Intensity of haemoglobin bands was enhanced by staining with napthyl blue black.

Since muscle tissue only was available from three specimens, both muscle and liver tissues of one individual of *C. penicillata* was examined, to establish the homology of observed staining patterns between the different tissue types.

Electromorphic alleles were described according to their relative mobilities on the gel, with the fastest (most anodal) being designated as A, and successively cathodal alleles being designated as B, C, D etc. Two approaches were taken in the analysis of the allozyme data: 1. analysis of allele frequencies, using the computer program BIOSYS-1 (SWOFFORD and SELANDER 1989); and 2. cladistic (parsimony) analysis of qualitative allozyme characters, using the computer program PAUP (SWOFFORD 1985). Computer programs were run on an IBM-compatible, XT personal computer.

Analysis of allele frequencis

From the individual genotypes at each locus (including monomorphic loci in which all individuals were scored as AA), allele frequencies were determined and used to calculate genetic distances and similarities (NEI's (1978) and D_N and I, and ROGERS' (1972) D_R and S) and mean heterozygosities ($\bar{H}$). In calculating $\bar{H}$, owing to the fact that localities were generally represented by single individuals (with the exception of the yellow mongoose, for which $\bar{H}$ was obtained from TAYLOR et al. 1990), data were pooled for each species. Genetic distances were summarised using both phenetic (unweighted pair group method with averages (UPGMA) phenogram: SNEATH and SOKAL 1973) and cladistic (distance WAGNER tree: FARRIS 1972) methods, for NEI's D_N and ROGERS' D_R values respectively. Analysis of allele frequency data was based on 17 loci, as missing data for GDH for three species prevented analysis of this locus.

Cladistic analysis of qualitative locus characters

Qualitative allozyme characters may be coded for cladistic analysis by: 1. treating alleles as characters and presence or absence of alleles as character states ("independent alleles model"); and 2. treating the locus as a character and alleles as character states. Although the first approach has the advantage of producing binary characters which are easily ordered using the outgroup method (WATROUS and WHEELER 1981), this method can hypothetically give rise to loci having no alleles, and BUTH (1984) recommends that the latter approach (treating the locus as character) should be used for cladistic analysis of allozyme data. Several models have been dscribed for ordering multisate locus characters (MICKEVICH and MITTER 1983), and BUTH (1984) recommends that researchers should explicitly state their ordering procedure. However, SWOFFORD (1985) suggests that there is no need to order multistate characters when there is no obvious evolutionary sequence (see also BEZY and SITES 1987; STASZ et al. 1989).

Table 1. **Species and locality data of specimens of eight African viverrid species analysed for allozyme electrophoresis**

Species and locality	n	Method[1]	Tissue[2]
Cynictis penicillata:			
Kaal Plaas Farm, Pretoria, Transvaal	3	T	L, K, H, M
Rhenosterfontein Farm, Cullinan, Transvaal	4	T, S	L, K, H, M
Karroo National Park, Cape Province	1	T	L, K, H, M
Windhoek, Namibia	4	T, R	L, K, H
Victoria West, Cape Province	5	T	L, K, H
Glen Agricultural Coll., Bloemfontein, OFS	15	T, S	L, K, B
Erfdeel Farm, Kroonstad, OFS	2	T	L, K
Riemvasmaak, northern Cape Province	1	T	L, K
Galerella sanguinea:			
Weenen Nature Reserve, Natal	1	T	L, K, M
Blydschap Private Nature Reserve, N. Trvl.	1	T	K, K, H, M
Galerella pulverulenta:			
Karroo National Park, Cape Province	1	T	L, K, H, M
Riemvasmaak, northern Cape Province	1	T	K, H
Atilax paludinosus:			
Hilton, Pietermaritzburg, Natal	1	R	L, K, H, M
Howick, Pietermaritzburg, Natal	1	R	M
Wagondrift Farm, western Cape	1	T	L, K, H, M
Herpestes ichneumon:			
Colchester Farm, Natal	1	R	M
Suricata suricatta:			
On N1, near Kimberley, Cape Province	1	R	L, K, H, M
Helogale parvula:			
Blydschap Private Nature Reserve, N. Trvl.	1	T	L, K, H, M
Genetta tigrina:			
Skewbridge, Pietermaritzburg, Natal	1	R	K, M
Blydschap Private Nature Reserve, N. Trvl.	2	T	L, K, H, M

[1] Methods of collections of specimens: T (live trapped); R (road kill); S (shot). – [2] Tissues collected: L (liver); K (kidney), H (heart); M (muscle); B (blood).

In the present study, the locus was recognised as character, and PAUP was performed on both ordered (using the "relative mobilities model": Mickevich and Mitter 1983) and unordered data, representing allelic variants at ten loci showing interspecific differences. All PAUP analyses were run with the options: MULPARS, SWAP=GLOBAL and ROOT=OUTGROUP, and the genet *Genetta tigrina* was taken as the outgroup. Analyses involving unordered data resulted in 97 equal length trees. A consensus tree, obtained from these trees using the CONTREE program of PAUP, was uninformative in producing an unresolved polychotomy involving six mongoose species. The analysis of ordered data produced six equal length trees, and a more completely resolved consensus tree. For this reason, only the results of the ordered character data are presented in this paper.

Results

Genetic heterozygosities and genetic distances

Of the 18 loci scored, 14 were polymorphic, either between or within species. Of these, ten loci showed consistent allelic differences between species or groups of species (Table 2). From Tables 2 and 3, no allelic variation was found in *Galerella pulverulenta* (Cape grey mongoose), *Atilax paludinosus* (water mongoose), *Herpestes ichneumon* (large grey mongoose), *Suricata suricatta* (suricate) and *Helogale parvula* (dwarf mongoose). Mean

Table 2. **Allelic designations of 14 polymorphic genetic loci for eight species of African Viverridae**
Abbreviations for species explained in Fig. 1. Abbreviations for loci explained in text

Locus	Species *Cp*	*Gs*	*Gp*	*Ap*	*Hi*	*Ss*	*Hp*	*Gt*
ALB	A	A	A	A	A	A	B	C
CAT	E, G, H	D, F	F	B	C	C	C	A
GDH	E	C	–	–	–	F	D	A, B
GOT-1	A, B	B	B	B	B	B	B	B
GOT-2	A, B	B	B	B	B	B	B	B
GPD	A, B	B	B	B	B	B	B	C
HB	E	C	C	C	C	B	A	D
IDH	A	B	A	A	A	A	A	A
MDH-1	B	B	B	B	B	B	B	A, B
MDH-2	A	A	A	B	A	A	A	B
ME	B	C	B	B	B	A	C	D, E
PGD	A, B, C	C	C	C	C	C	C	C
PGM	A, C	C	C	C	C	C	C	B
SOD	B	B	B	B	B	B	A	B

Table 3. **Estimates of percentage polymorphic loci (%P), mean heterozygosity ($\overline{H}$), and standard error (s.e.) of $\overline{H}$ in eight species of Viverridae**
(data for *Cynictis penicillata* represent the mean for eight populations and were taken from a separate study: Taylor et al. 1990)

Species	N[1]	%P	$\overline{H}$	s.e.
Cynictis penicillata	29.3	6.8	0.026	0.020
Galerella sanguinea	2.0	5.9	0.039	0.039
Galerella pulverulenta	2.0	0	0	0
Atilax paludinosus	2.8	0	0	0
Herpestes ichneumon	1.0	0	0	0
Suricata suricatta	1.0	0	0	0
Helogale parvula	1.0	0	0	0
Genetta tigrina	2.8	11.8	0.051	0.036

[1] Mean sample size per locus.

heterozygosity ($\overline{H}$) was 0.026 in *Cynictis penicillata* (yellow mongoose); 0.039 in *Galerella sanguinea* (slender mongoose); and 0.051 in *Genetta tigrina* (genet; Table 3).

Nei's D_N varies from 0.06 (between *G. pulverulenta* and *H. ichneumon*) to 0.63 (between *G. tigrina* and *S. suricatta*), with a mean of 0.30. Rogers' D_R varies from 0.06 (between *G. pulverulenta* and *H. ichneumon*) to 0.47 (between *G. tigrina* and *S. suricatta*), with a mean of 0.26 (Table 4). The UPGMA phenogram, based on D_N (Fig. 1A), indicates the genetic separatedness of the genets (Viverrinae) from the mongooses (Herpestinae), at a distance of 0.53. Beyond this, no clear groupings are evident, and most splitting events appear to occur over a rather narrow range of genetic distances. The solitary species (*Herpestes, Galerella* and *Atilax*) and the semi-social *Cynictis* are loosely grouped together genetically, and the social species (*Helogale, Suricata*) appear somewhat distinct.

The topology of the outgroup-rooted, distance Wagner trees (Figs. 1B, 1C) is different from the UPGMA phenogram (Fig. 1A). Figure 1B was based on the same data as the UPGMA phenogram. Figure 1C was "optimised" by recording the allelic character states at the ME locus so as to eliminate an obvious convergence (the shared possession of allele C in *G. sanguineus* and *H. parvula*): allele C in *H. parvula* was recoded as D and alleles D and E were recoded as E and F respectively. The "optimised" tree had a "f" value (Farris

Table 4. **Values of (A) Nei's (1978) genetic distance (below diagonal) and identity (above the diagonal), and (B) Rogers' (19072) genetic distance (below the diagonal) and similarity (above the diagonal), between eight species of Southern African Viverridae**

	Cp	*Gs*	*Gp*	*Ap*	*Hi*	*Ss*	*Hp*	*Gt*
A								
Cp	–	0.78	0.88	0.83	0.88	0.77	0.77	0.60
Gs	0.25	–	0.87	0.78	0.84	0.72	0.78	0.54
Gp	0.12	0.14	–	0.88	0.94	0.76	0.76	0.59
Ap	0.19	0.25	0.12	–	0.88	0.71	0.71	0.65
Hi	0.12	0.17	0.06	0.12	–	0.82	0.82	0.59
Ss	0.27	0.33	0.27	0.35	0.19	–	0.76	0.53
Hp	0.27	0.25	0.27	0.35	0.19	0.27	–	0.59
Gt	0.52	0.61	0.52	0.42	0.52	0.63	0.52	–
B								
Cp	–	0.77	0.88	0.82	0.88	0.76	0.76	0.58
Gs	0.23	–	0.85	0.77	0.83	0.71	0.77	0.53
Gp	0.12	0.15	–	0.88	0.94	0.76	0.76	0.58
Ap	0.18	0.23	0.12	–	0.88	0.71	0.71	0.64
Hi	0.12	0.17	0.06	0.12	–	0.82	0.82	0.58
Ss	0.24	0.29	0.24	0.29	0.18	–	0.76	0.53
Hp	0.24	0.23	0.24	0.29	0.18	0.24	–	0.58
Gt	0.42	0.47	0.42	0.36	0.42	0.47	0.42	–

Fig. 1. UPGMA tree (A) and "unoptimised" (B) and "optimised" (C) distance Wagner trees, based on allele frequencies from 17 genetic loci in eight species of Southern African Viverridae. Distance Wagner trees were outgroup-rooted taking the genet *Genetta tigrina* as the outgroup. The procedure for "optimising" the distance Wagner tree in (C) is explained in the text. Abbreviations for species as follows: Ap = *Atilax paludinosus* (water mongoose); Cp = *Cynictis penicillata* (yellow mongoose); Gp = *Galerella pulverulenta* (Cape grey mongoose); Gs = *Galerella sanguinea* (slender mongoose); Gt = *Genetta tigrina* (large-spotted genet); Hi = *Herpestes ichneumon* (large grey mongoose); Hp = *Helogale parvula* (dwarf mongoose); Ss = *Suricata suricatta* (suricate)

1972) of 0.654 and a cophenetic correlation coefficient of 0.965, compared to a "f" value of 1.121 and a cophenetic correlation coefficient of 0.930 in the "unoptimised" tree.

Both distance Wagner trees resulted in the early splitting off of *Atilax*, and the subsequent trichotomous split. In the "unoptimised" tree these three lineages comprise: 1. *Cynictis*; 2. *Galerella*, and the two social genera, *Helogale* and *Suricata*; 3. *Herpestes*. In the "optimised" tree the three lineages comprise: 1. all the social species (*Cynictis, Helogale, Suricata*); 2. *Galerella*; 3. *Herpestes*.

Phylogenetic analysis of discrete allozyme characters

Figure 2A shows one of six trees produced by parsimony, cladistic analysis (PAUP) of ordered, multistate locus characters (the data on which this analysis was based are shown in Table 5). All six trees had a length of 27 and a consistency index of 0.815. Character state changes (i.e. apomorphies) have been superimposed on the tree in Fig. 2A, and homoplasies are indicated by underlining. Figure 2B shows the strict consensus tree obtained from these six trees. Areas of instability, as indicated by unresolved trichotomies on the consensus tree, concern the resolution of the three social species (three of the six trees

Table 5. **Ordered allozyme locus characters used in parsimony cladistic analysis (PAUP) of seven Southern African mongoose species**

Species	ALB	CAT	GDH	HB	IDH	MDH-2	ME	PGM	SOD	GPD
Cp	2	3	3	2	0	1	2	1	0	1
Gs	2	4	1	1	1	1	1	1	0	1
Gp	2	4	–	1	0	1	2	1	0	1
Ap	2	1	–	1	0	0	2	1	0	1
Hi	2	2	–	1	0	1	2	1	0	1
Ss	2	2	4	3	0	1	3	1	1	1
Hp	1	2	2	4	0	1	1	1	0	1
Gt	0	0	0	0	0	0	0	0	0	0

Trees were outgroup-rooted, taking the genet *Genetta tigrina* as the outgroup. Character states (alleles) were ordered using the "relative mobility model", which assumes that alleles closer in mobility on a gel to the allelic state possessed by the outgroup are more primitive than alleles which are further away from the outgroup allele state. Abbreviations of loci explained in text.

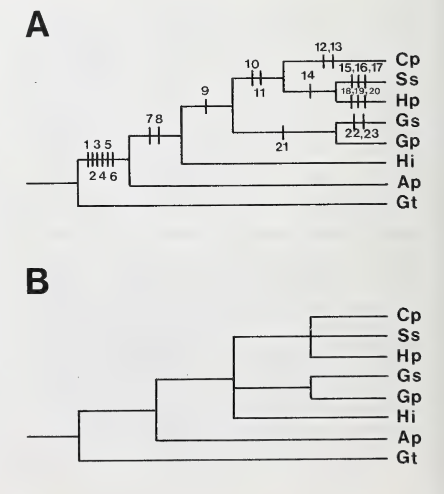


Fig. 2. Cladograms of seven Southern African mongoose species, resulting from phylogenetic analysis using parsimony (PAUP package) of allozyme data, using loci as characters and alleles as character states. Abbreviations for species given in Fig. 1. A: One of six, equal length, most parsimonious cladograms (length = 27; consistency index = 0.815); B: Consensus tree resulting from the six most parsimonious cladograms. Numbers on cladogram (A) represent character state changes as follows (abbreviations of loci explained in text): 1 = GPD (0 → 1); 2 = PGM (0 → 1); 3 = ME (0 → 2); 4 = HB (0 → 1); 5 = CAT (0 → 1); 6 = ALB (0 → 2); 7 = MDH-2 (0 → 1); 8 = CAT (1 → 2); 9 = GDH (0 → 1); 10 = HB (1 → 2); 11 = GDH (1 → 2); 12 = GDH (2 → 3); 13 = CAT (2 → 3); 14 = HB (2 → 3); 15 = SOD (0 → 1); 16 = ME (2 → 3); 17 = GDH (2 → 4); 18 = ME (2 → 1); 19 = HB (3 → 4); 20 = ALB (2 → 1); 21 = CAT (2 → 4); 22 = ME (2 → 1); 23 = IDH (0 → 1)

supported a *Suricata-Helogale* clad, while the other three supported a *Cynictis-Suricata* clade), and the recognition of a *Galerella-Cynictis-Helogale-Suricata* clade (supported by two trees).

The consensus tree in Fig. 2B is similar in overall topology to the "optimised" distance Wagner tree (Fig. 1C), in recognising the early separation of *Atilax*, and the subsequent trichotomy involving the same three lineages (social species, *Galerella* and *Herpestes*).

Discussion

Genetic distance analyses

Allelic variation within species was minimal (**H** = 0–0.051: Table 3). For the ten loci that showed between-species polymorphism, the pattern of distribution of alleles was species and group specific (Table 2). Species differed from one another therefore, in the presence or absence of alleles rather than in allele frequency. These factors promote the stability of dendrograms based on genetic distances (particularly when sample sizes are very small), as shown by Archie et al. (1989), and they also provide suitable qualitative characters for cladistic analysis.

Nei's (1978) genetic identity values (I) between pairs of viverrid species (including the genet *G. tigrina*: Table 4) invariably exceed the mean value for congeneric species given by Thorpe (1982: I=0.54, s.d.=0.17, **n**=824). I values between species of mongooses (Table 4) generally exceed the mean value for incipient species of mammals, given by Ayala (1975: I=0.77). These results suggest a recent radiation of the Viverridae, and are rather surprising, given the fact that mongooses and genets are separated at the subfamily level (or the family level: Wozencaft 1989b), and that most of the species of mongooses included in this study represent separate genera.

However, palaeontological and morphological data provide support for a recent, and somewhat "explosive", radiation of African herpestines. Three lineages of mongooses were present in the Pliocene Langebaanweg deposits, a *Galerella*-type form, a *Herpestes*-type form and a *Mungos*-type form (Hendey 1974, and unpub. data). The close resemblance of the *Mungos* form to *Herpestes* suggested that these two lineages had only recently split (Hendey 1974; furthermore, earlier fossil herpestines are represented only by unspecialised *Herpestes*-type forms: Savage 1978). By the early Pleistocene, fossil representatives of all the extant genera had appeared (Hendey 1974; Savage 1978). On the basis of dental characters and fossile evidence, Petter (1969) suggested a recent origin of the extant African Viverridae. Further allozyme analyses, based on larger numbers of loci, species and specimens, are needed to verify the apparently high genetic similarity between viverrid species.

Comparison of phenetic and cladistic allozyme approaches

Although the two species of *Galerella* are not clustered together on the UPGMA phenogram, they are cladistically similar as shown by the "optimised" distance Wagner (Fig. 1C) and PAUP (Fig. 2) trees. The UPGMA phenogram in Fig. 1A shows a close genetic relationship between *Galerella pulverulenta* and *Herpestes ichneumon* (the two species are separated by a D_N of only 0.06), which would appear to support the argument for including *Galerella* in *Herpestes* (Wozencraft 1989). However, the "optimised" distance Wagner tree (Fig. 1C) and the PAUP consensus tree (Fig. 2B) show *Herpestes* and *Galerella* to be distinct lineages which separated at the same time as the origin of the "social" lineage. The trichotomous split on the cladistic trees in Fig. 1C and Fig. 2 is supported by palaeontological evidence, which shows the existence of three lineages of mongooses in Langebaanweg deposits (3–5 MYA): a *Galerella*-type form, a *Herpestes*-type form and a *Mungos*-type (i.e. social) form (Hendey 1974, and unpub. data).

Buth (1984) has pointed out that UPGMA trees based on electrophoretic data represent the true phylogeny only when the assumption of equal rates of evolution in different lineages is met. The marked difference in topology between the UPGMA phenogram and the cladistic (i.e. distance Wagner and PAUP) trees in this study results from unequal rates of evolution in different lineages of mongooses, as is evident from the distance Wagner trees (Figs. 1B, 1C) and the PAUP tree in Fig. 2A. A similar explanation was given for conflicting phenetic and cladistic analyses of electrophoretic data by Baverstock et al. (1979) and Hillis (1985). Anagenic change (as measured by branch length in the distance Wagner trees in Fig. 1, or by the number of character stage changes in Fig. 2A) appears to occur at a faster rate in the "advanced", social mongooses (*Suricata, Helogale, Cynictis*) than in the "primitive", solitary species (*Galerella, Herpestes, Atilax*), giving rise to an UPGMA tree in which the social species appear to split off before the origin of the extant solitary species. The genetic similarity between *Herpestes, Galerella, Atilax* and *Cynictis* on the UPGMA phenogram is clearly a result of symplesiomorphic (i.e. shared primitive) characters (see Fig. 2A).

Comparison of allozyme and other data sets

Figure 3 illustrates six previous phylogenetic schemes for the Herpestinae, based on morphological, palaeontological, karyological and behavioral evidence. From Fig. 3, there is clearly little consensus regarding phylogenetic relationships among the mongooses. However certain comparisons can be made between the various published phylogenetic schemes and the allozyme trees presented in the present study.

The "optimised" distance Wagner tree (Fig. 1C) and PAUP trees (Fig. 2) support a phylogenetic split between the social and the solitary mongooses. This conclusion is supported by karyological (Fredga 1972), palaeontological (Hendey 1974), and morphological (Gregory and Hellman 1939) evidence (Fig. 3), although Hendey (1974) and Gregory and Hellman (1939) place the "semi-social" genus *Cynictis* closer to *Galerella* than to the social species (Fig. 3A, D). In this respect, from the cladistic analyses of the allozyme data, *Cynictis* separates first from the "social" lineage, and therefore shares greater symplesiomorphic similarity with *Galerella* than do *Helogale* and *Suricata* (this is reflected in the position of *Cynictis* on the UPGMA phenogram in Fig. 1A). Baker (1987) groups *Helogale, Mungos* and *Cynictis* on behavioral grounds, while maintaining that *Suricata* is behaviorally unique (Fig. 3E). However, these behavioral differences in *Suricata* are clearly autapomorphies, and, cladistically speaking, *Suricata* would probably be grouped with *Helogale* and *Mungos* on behavioral grounds.

The close genetic similarity between *Atilax, Herpestes* and *Galerella* (Fig. 1A) is supported by phenetic analyses of behavioral and morphological data (Baker 1987: Fig. 3E, F). However, as shown in the cladistic allozyme trees, and as discussed above, this similarity is symplesiomorphic in nature. The phylogenetic separation of the *Galerella* and *Herpestes* lineages, as suggested by the cladistic, allozyme trees (Figs. 1B, 1C, 2), is supported by palaeontological (Hendey 1974), morphological (Gregory and Hellman 1939; Petter 1969) and karyological (Fredga 1972) data (see Fig. 3). As mentioned above, these results argue against the inclusion of *Galerella* in *Herpestes*, as suggested by Wozencraft (1989b).

Baker (1987) has suggested the possibility of an *Atilax*-like ancestor of the Herpestinae, an idea that is supported by cladistic analysis of allozymes in the present study (Figs. 1B, 1C, 2). Although the earliest mongoose fossils, from the Miocene in Africa and Europe, are generally recognised as unspecialised *Herpestes*-type forms (Savage 1978), a diverse array of these primitive viverrid genera existed during the Miocene, of which many lineages became extinct (e.g. *Kichechia, Leptoplesictis, Herpestides, Legetetia:* Schmidt-Kittler 1987). There need not therefore have been a direct line of descent form the earliest

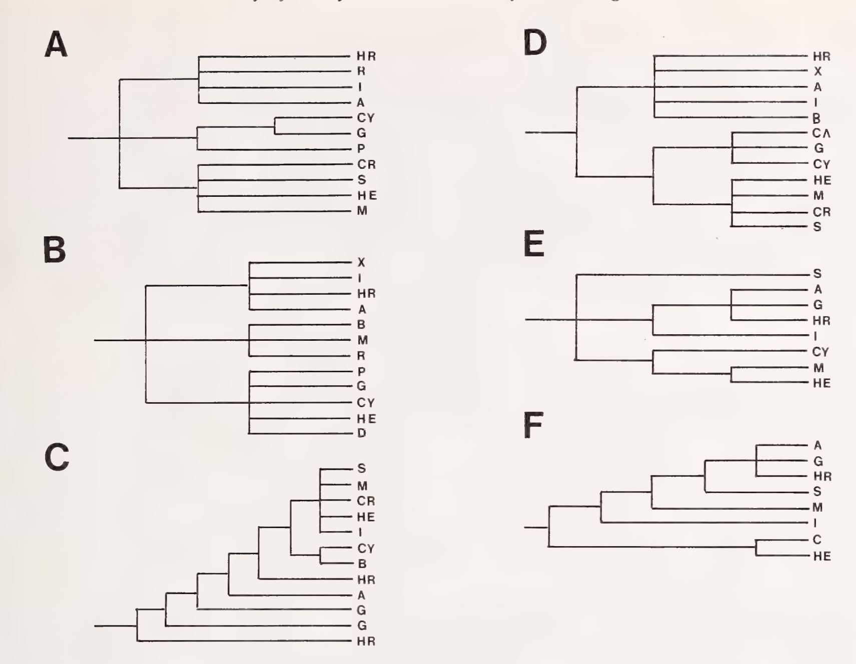


Fig. 3. Dendrograms summarising relationships among genera of mongooses (Hepestinae), based on independent, published studies involving different suites of characters. A: based on palaeontological data, in HENDEY (1974, and unpublished phylogenetic tree); B: based on groups identified by PETTER (1969) on the basis of size and dental characters; C: modified from FREDGA (1972), on the basis of karyological data; D: modified from GREGORY and HELLMAN (1939), based on characters of the skull and teeth; E: based on phenogram from behavior data (BAKER 1987); F: based on phenogram from morphological data (BAKER 1987). Abbreviations of genera are as follows: A = *Atilax*; B = *Bdeogale*; CA = *Calogale*; CR = *Crossarchus*; CY = *Cynictis*; D = *Dologale*; G = *Galerella*; HR = *Herpestes*; HE = *Helogale*; I = *Ichneumia*; M = *Mungos*; P = *Paracynictis*; R = *Rhynchogale*; S = *Suricata*; X = *Xenogale*

unspecialised viverrids to all of the extant species (HENDEY, pers. comm.), and it is quite plausible that a more recent *Atilax*-like ancestoral species gave rise to the apparently recent (Pliocene and early Pleistocene) extant mongoose radiation.

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Zusammenfassung

Untersuchungen zur Evolution afrikanischer Mangusten (Viverridae: Herpestinae) aufgrund von Allozymen

Durch waagerechte Stärkegel-Elektrophorese wurden die Unterschiede der Allozyme an 18 Proteinloci bei 48 Exemplaren von sieben Mangustenarten (Viverridae: Herpestinae: *Cynictis penicillata, Helogale parvula, Suricata suricatta, Atilax paludinosus, Herpestes ichneumon, Galerella sanguinea* and *G. pulverulenta*) und bei einer Ginsterkatze (Viverridae: Viverrinae: *Genetta tigrina*) untersucht.

14 Loci waren polymorph und 10 waren zwischenartlich unterschiedlich. Eine phenetische Analyse der genetischen Abstände (NEI 1978) deutet auf eine verhältnismäßig junge "explosive" Artenbildung der untersuchten Viverridae. Kladistische Analysen (wobei *Genetta tigrina* als Außengruppe betrachtet wurde) die durch "Wagner-Bäume" der genetischen Abstände (ROGERS 1972) und Sparsamkeitsanalyse geordneter Eigenschaften multipler Loci gewonnen wurden, ergaben übereinstimmende Dendrogramme, die eine frühe Abzweigung von *Atilax* zeigen, mit einer darauffolgenden Aufspaltung in die drei Stämme: 1. *Galerella*, 2. *Herpestes* und 3. eine Gruppe sozialer Arten mit *Helogale, Suricata* und *Cynictis*. Diese Befunde werden durch paläontologische, morphologische, karyologische und ethologische Vergleiche gestützt. Wegen ungleicher Veränderungsgeschwindigkeiten der verschiedenen Linien, führten die phenetischen und kladistischen Analysen der Allozyme zu widersprüchlichen Dendrogrammen. Der kladistischen Methode wird für die Ermittlung phylogenetischer Beziehungen hier der Vorrang gegeben.

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Reproduction in the European lynx, *Lynx lynx*

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Abstract

Based on skinned carcasses collected in Norway from 1960 through 1976. The mating period lasted from February through early April, with a peak of mating activity in March. Parturition occurred in late May and early June. Normal litter size was 2–3. Males were normally sexually mature at 2¾ years of age, but some males were mature at 1¾ years of age. Females were sexually mature at 1¾ years of age, but the investigation also indicated maturation in approximately 50 % of the females at ¾ years of age.

Introduction

Reproduction is one of the major factors controlling development of the population structure. Since population biology of the European lynx, *Lynx lynx*, has not been studied closely before, and these aspects are very important for management purposes, it was mandatory from 1960 to 1980 for the payment of the Norwegian state bounty on lynxes that all skinned carcass be sent to the Directorate for Nature Management for investigation and assessment. This investigation is based on samples accumulated from 1960 through 1976.

Material and methods

The investigated material comprised testes from 149 males and reproductive tracts including ovaries from 176 females. Embryos from 8 reproductive tracts were also examined. Since the reproductive organs has been stored in 70 % ethanol for a number of years, they were very hard and shrunken, and were therefore not suitable for immediate sectioning. In an effort to soften tissues and aid rehydration the material was treated with a mixture of 2/3 glacial acetic acid and 1/3 glycerol (Baker 1966). A solution consisting of equal parts of 1 % trisodium phosphate and 10 % sodium hydroxide was used to induce swelling of the organs and to stabilize them for sectioning as well as to neutralize the effect of acetic acid (Cleave and Ross 1947; Löwegren 1960).

Analysis of testes

Due to partial decay as well as a result of storage in 70 % alcohol, the testes material was in very bad histological condition. Microscopic observation of sperm and spermatids was very difficult. Fertility could be decided by this method in only a few cases.

Testes of seasonal breeders normally vary in size and weight with the reproduction cycle of the species. They are normally also larger and heavier in sexually mature animals than in the immature (Nalbandov 1976). The testes were weighed after the swelling process. They were impossible to separate from the surrounding tissue before swelling. In this paper testes weight means weight of testes including epididymis and tunica vaginalis. Some pairs of testes were very different in size as only one testicle was functional. Weight of the largest testicle in one specimen has therefore been used in the following comparisons, referred to as testis weight.

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Analysis of ovaries

Ovaries were macroscopically examined for form, colour, size and stage of development, then sectioned with a freezing microtome and stained with Heidenhain's haematoxylin (Romeis 1948; Baker 1966). Sections were analysed with a microscope, and Graafian follicles and corpora lutea were counted. Fresh luteal bodies are found throughout the year. Normally they are easily recognizable from luteal bodies of the previous cycle (Crowe 1975) based on difference in colour and consistency. Fresh luteal bodies are light yellow. One year later, when they turn into "lutein bodies of the previous cycle", they are red-brown or gray with a significantly less granular appearance than fresh luteal bodies. Luteal bodies from three cycles have been observed in eight cases. Ovulation rates were calculated by counting the fresh luteal bodies and Graafian follicles in ovaries (Cheatum 1949; Duke 1949; Gashwiler et al. 1961).

Analysis of uterine tracts and embryos

Uterine tracts were opened lengthwise and held up to a bright light to ascertain the presence of placental scars and evidence of resorbing embryos (Saunders 1961). This method proved inappropriate for histological inspection of the present material, due to damage by shrinking after storing in 70 % alcohol. The reproductive tracts smaller than 40 g were induced to swell along with the ovaries. They were weighed after storage in 8 % formaldehyde for one year after swelling. Obviously pregnant reproductive tracts, heavier than 100 g were not induced to swell, since due to storing in formaldehyde they were not shrunken. Embryos were weighed and crown-rump lengths were measured in the manner described by Arey (1965).

Age of embryos

Approximate age of embryo litters was determined by comparing weights and lengths with a prenatal growth curve prepared for the Canada lynx from Newfoundland *Lynx canadensis subsolanus* by Saunders (1961). His table on development of embryos of known age in domestic cats *Felix catus* based on data from Dawson (1941), Windle and Griffin (1931), Coronios (1933) and Worden and Lane-Peter (1957), was established for aging the Canada lynx embryos of unknown age. With approximate age of litters established, it was possible to calculate approximate dates of conception and parturition. In these calculations the gestation period was considered to be 70 days (Lindemann 1955).

Masting period

The period of reproductive activity was determined by comparing time of the year with weights of testes, ovaries and uterine tracts, as well as with ovulation stage as obtained by analysis of ovaries. Males younger than 31 months and females younger than 20 months were eliminated to avoid bias due to low weights in immature specimens (Lindemann 1955). Age in months refer to an estimated birth date of May 15, based on information published by Lindemann (1956), Haglund (1966) and Zuckermann (1952). Age was determined by means of incremental lines in tooth cementum (Kvam 1984).

Sexual maturation

To determine the age of sexual maturation, age was compared with weights of testes, ovaries and uterine tracts, and with reproductive status obtained from analysis of ovaries. Only specimens caught in the mating period, January through April (Birkeland 1971), were taken into consideration.

Results

Analysis of ovaries

In 104 females which had ovulated, the ovulation rate was 3.10 ± SE 0.16 (range: 1–10). Mean ovulation rate in 8 evidently pregnant females was 2.88 ± SD 0.64 (range: 2–4). Ovulation rates were not significantly different in pregnant and non pregnant females: U=3822.5, P=0.985 (Mann-Whitney test). In females over 2 years of age there were no significant differences concerning ovulation rates between age classes or between years of death (Kvam 1990).

Mating and parturition

A. Males: Weights of testes varied little throughout the year. There was a tendency to increased weights of testes in February through May. Individual differences within each month were significant, however. Lack of material from June throughout October was a great disavantage. The rutting season of the males could not be defined accurately based on this investigation (See Fig. 1).

B. Females: Weights of ovary were low in January and February, but a tendency to increase was observed from March throughout may. Weights of uterine tracts tended to remain constant throughout the year, however there was an obvious increase in March and April, culminating in a peak in May. A narrow mating period cannot be defined based on weights of ovaries and uterine tracts from such a small sample (94 ovaries and 119 uterine tracts).

The mating period seems to be rather prolonged. It starts in January, but the majority

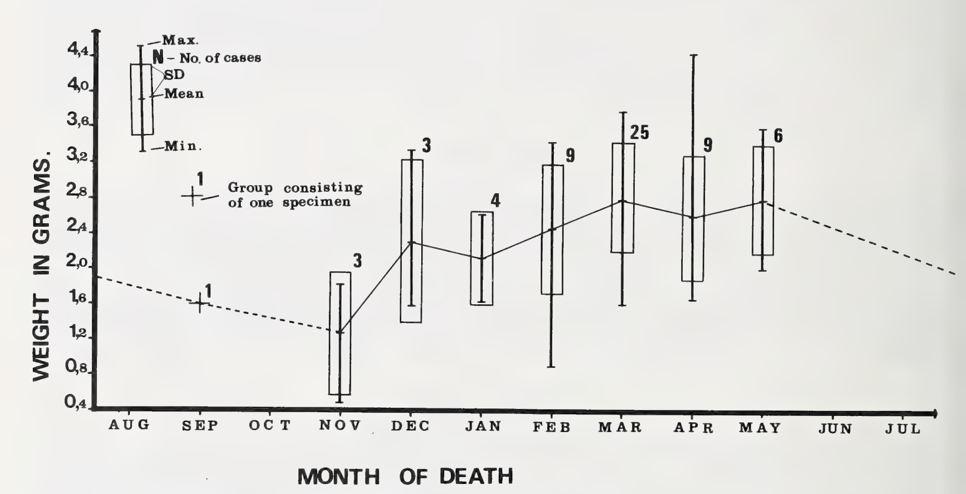


Fig. 1. Weight of the largest testicle in relation to month of death in males older than 31 months of age

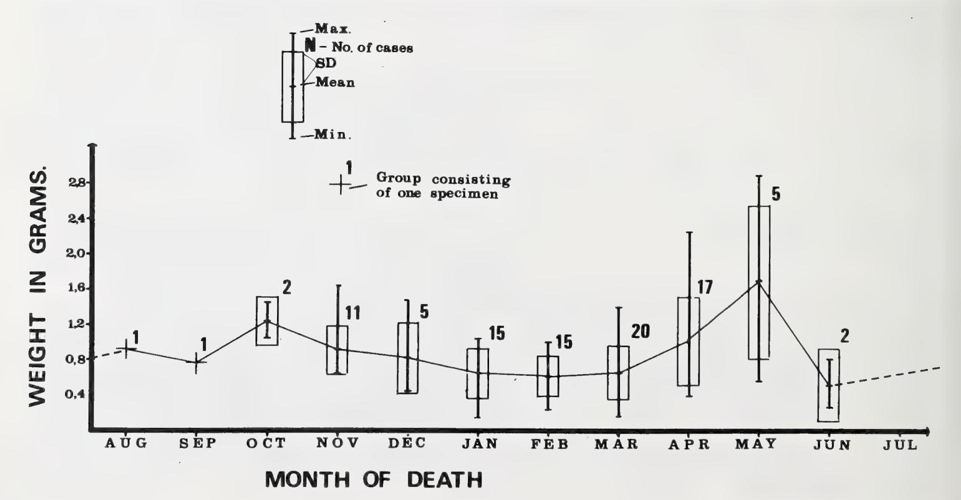


Fig. 2. Weight of the largest ovary in relation to month of death in females older than 20 months of age

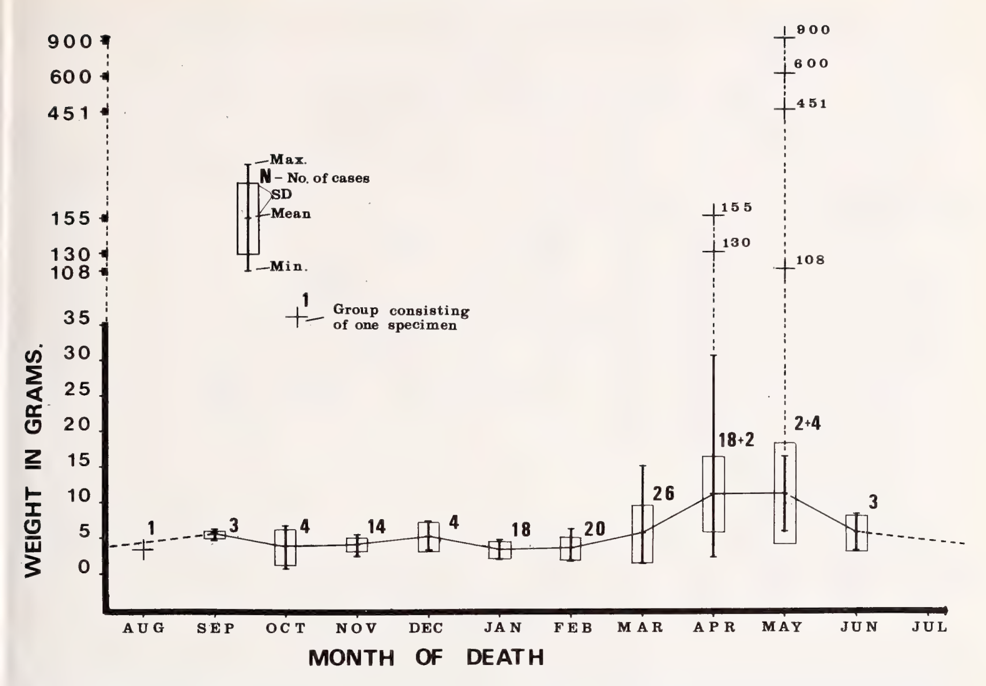


Fig. 3. Weight of uterine tract in relation to month of death in females older than 20 months of age

of ovulations seems to take place in February and March. In early April the season of heat appears to be over in most females (Tab. 1). Conception dates based on known date of shooting and approximate age of embryos are shown in Table 2. The conception period was estimated as March 21 through April 9 with a median conception date of March 25. The corresponding parturition period was May 29 through June 18, and median parturition date was June 3. Mean number of embryos in the 8 obviously pregnant uterine tracts was 2.50 ± SD 0.53. Range: 2–3 (Tab. 3).

Conclusion: All results concerning time of mating season, suggest February, March and early April. The data from the examined ovaries indicate mating tending to be spread throughout the indicated period of two to three months. Parturition seems to take place during late May or early June.

Sexual maturation

A. Males: Variation in testes weights within age classes was pronounced. (F=51.58, P=0.00, d.f.=4, N=86, One way procedure). A tendency to stabilize was noticeable from 2¾ years of age (Fig. 4). The age class ¾ years (7.5–11.5 months) showed significantly lower testes weights than all older age classes (P>0.05, Tukey test). Testes weights in the 1¾-year age class (19.5–23.5 months) were significantly lower than in males older than 3¾ years (P>0.005, Tukey test).

The low testes weights indicate that ¾-year-old males are usually immature.The 1¾-year-old (19.5–23.5 months) males with lowest testes weights are presumed to be immature. Most of 1¾-year-old males showed testes weights comparable with older age classes: Seven specimens (21.2 %) showed testes weights higher than 2.67 g, which was the mean testes weight in all older males. Thirteen specimens (52 %) showed testes weights higher than mean testes weight in all older males minus 1 SD (2.04 g). These animals were

Table 1. **Data on examined ovaries in relation to month of death in females older than 20 months of age**

Per cent values. No. of cases in brackets

Developmental status	Month of death				
	Jan.	Feb.	Mar.	Apr.	May–Dec.
No ovulation since last year's period of heat. No large follicles.	59 (10)	12 (2)	–	5 (1)	–
No ovulation since last year's period of heat. Follicles diam. > 1 mm.	18 (3)	18 (3)	5 (1)	–	–
Fresh luteal bodies from this year's period of heat. Large follicles. Diam. > 1 mm	6 (1)	18 (3)	40 (8)	10 (2)	13 (4)
Fresh luteal bodies from this year's period of heat. Graafian follicles.	–	6 (1)	5 (1)	–	–
Fresh luteal bodies from this year's period of heat. No large follicles.	18 (3)	47 (8)	50 (10)	85 (17)	87 (27)
	(17)	(17)	(20)	(20)	(31)

Table 2. **Estimated dates of conception on and birth dates for the fetus material, based on a 70-day gestation period**

Date of kill	Age in days	Estimated date of conception	Estimated date of birth
13 Apr	20	24 Mar	2 Jun
4 May	25	9 Apr	18 Jun
23 Apr	26–30	24 Mar–28 Mar	2 Jun– 6 Jun
4 Apr	26–30	28 Mar–01 Apr	6 Jun–10 Jun
1 May	35–42	20 Mar–27 Mar	29 May– 5 Jun
15 May	50	26 Mar	4 Jun
28 May	68	21 Mar	30 May
31 May	68	24 Mar	2 Jun

Table 3. **Crown-rump length and weight of fetus in European lynx, *L. l. lynx* from Norway of unknown age**

Age is etimated by comparison with a development table for Canada lynx, *L. l. subsolanus* and domestic cat *F. catus* presented by Saunders (1961)

Estimated age in days after mating	Crown-rump length range (mm)	Weight[1] range (g)	Litter size
20	7.0–10.0	0.4	2
25	19.0–20.0	0.7–1.0	3
26–30	21.4–27.4	1.2–1.7	3
26–30	26.5–29.8	1.4–1.6	2
35–42	67.2	9.1–9.2	2
50	86.4–93.0	44.6–50.0	3
68	170.0–180.0	268.4–308.9	3
68	200.0	343.0–356.2	2

[1] Weight of individual embryos.

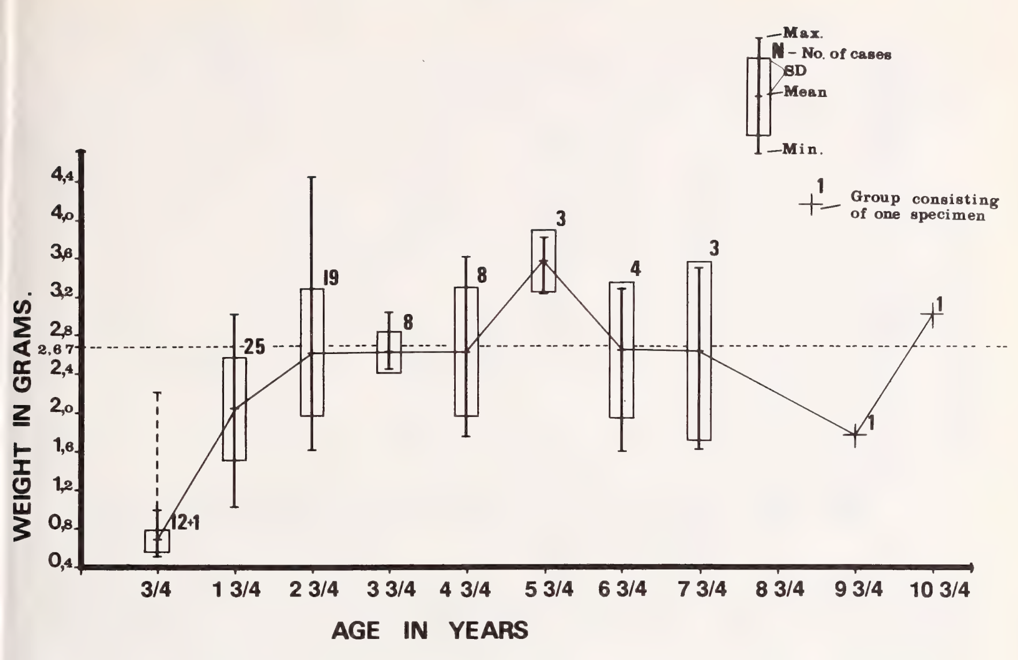


Fig. 4. Weight of the largest testicle related to age in males shot in the mating period (January throughout April). Mean weight of largest testicle in males older than 2¾ years is indicated by a dotted line

presumed to be fertile. 2¾-year-old males (31.5–35.5 months) do not differ significantly from older males, indicating 2¾-year-old males to be fully fertile.

Conclusions: The above outlined results thus indicate:

¾-year-old males (7.5–11.5 months): normally immature.

1¾-year-old males (19.5–23.5 months): approximately 50 % fertile.

2¾-year-old males (31.5–35.5 months): normally fertile.

B. Females: Variation in weights of ovary within age classes was pronounced (F=32.74, P=0.00, d.f.=4, N=81. One way procedure). ¾-year-old females showed stable and low values. There were significant differencs at the 0.05 level between ¾-year-old females and all older age classes (Tukey test). The 1¾-year-old females were different from the 3¾-year-old age class and the age class older than 3¾ years (P>0.05, Tukey test).

The largest ovary of No. 12/72 weighed 0.28 g, which was the lowest value recorded in 6-year-old females. This specimen was fertile, according to the ovary inspection record, even if weights of its largest ovary was comparable to the mean value in the ¾-year age class. This finding illustrates the danger to determine which females are fertile based on ovary weights alone. However, ovary weights can be of value to support results obtained by other methods.

¾-year-old females showed low weights and uterine tracts weights significantly different from uterine weights in older age-classes (P>0.05, Tukey test). Uterine weights in 1¾-year-old females were significantly different from uterine weights in all females older than 3¾ years (P>0.05, Tukey test). The minimum value in the 1¾-year age class was 1.38 g, but this specimen was immature. Between this minimum value and the second lowest uterine weight in immature 1¾-year-old females, uterine tracts of 6 specimens are recorded which, according to records from inspection of ovaries, were mature. All these values rank lower than mean weight plus 1 SD of the ¾-year age class. Maximum uterine weight in immature 1¾-year-old females was 3.34 g, which is comparable to the mean

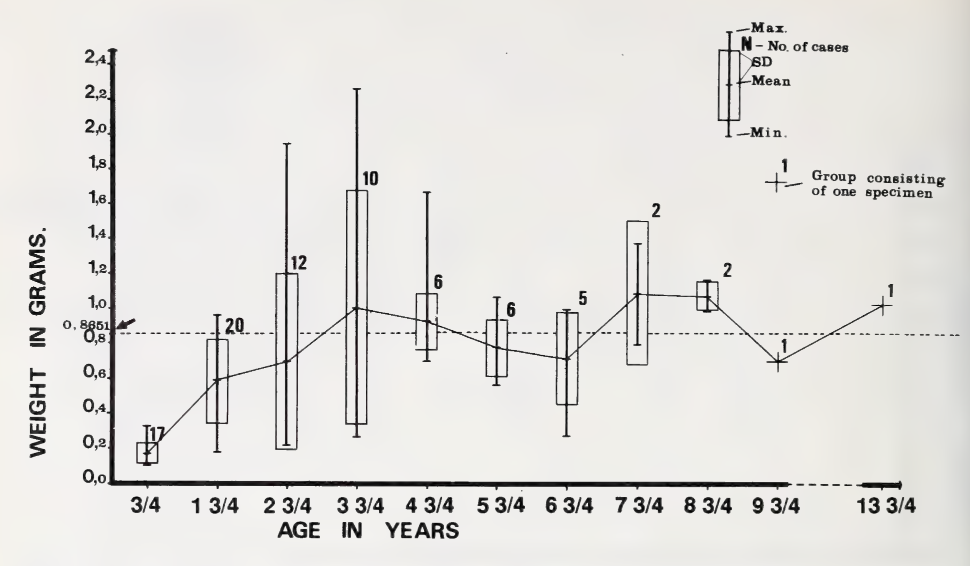


Fig. 5. Weight of the largest ovary related to age in females shot in the mating period (January throughout April). Mean weight of largest ovary in females older than 2¾ years is indicated by a dotted line

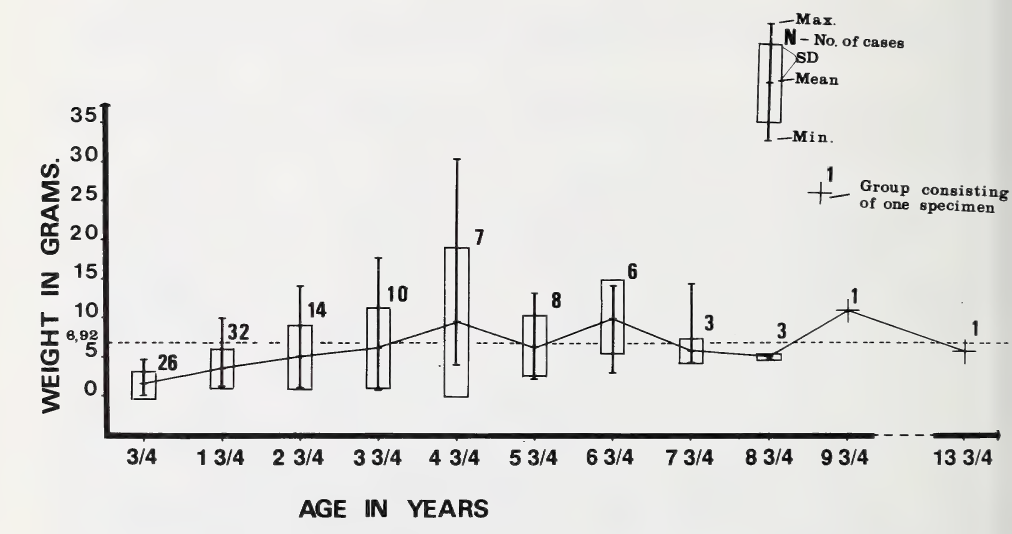


Fig. 6. Weight of uterine tract related to age in females shot in the mating period (January throughout April). Mean weight of uterine tract in females older than 2¾ years is indicated by a dotted line. Uterine tracts of two pregnant females shot in April were not included since their size was divergent from the remaining material

value of the age class. This implies that a female's maturity cannot be based on uterine weight alone, since mature and immature specimens overlap to a great extent.

The youngest female with luteal bodies was shot on April 4 at an age of 10.5 months. This specimen possessed 2 fresh luteal bodies, but its uterine tract was not turgid. Graafian follicles were detected in two ¾-year-old females. They were shot on April 4 to 9,

Table 4. **Age of sexual maturation in females given in percent based on examination of ovaries**
No. of cases in brackets

Maturation Age	Age in months 0–9,5	9,5–21,5	21,5–33,5	33,5–45,5	45,5–57,5
0	100 (24)	49 (17)	12 (3)	5 (1)	–
¾	–	51 (18)	28 (7)	14 (3)	–
1¾	–	–	48 (12)	43 (9)	–
2¾	–	–	–	33 (7)	–
3¾	–	–	–	–	6 (1)
1¾?	–	–	8 (2)	–	–
2¾?	–	–	4 (1)	5 (1)	69 (11)
3¾?	–	–	–	–	6 (1)
4¾?	–	–	–	–	19 (3)
Immature	100 (24)	49 (17)	12 (3)	5 (1)	–
Mature	–	51 (18)	88 (22)	95 (20)	100 (16)

0: Immature
¾: Maturation at ¾ years of age.
1¾: Maturation at 1¾ years of age.
2¾: Maturation at 2¾ years of age.
3¾: Maturation at 3¾ years of age.
1¾?: Mature at 1¾ years of age. Maturation age uncertain.
2¾?: Mature at 2¾ years of age. Maturation age uncertain.
3¾?: Mature at 3¾ years of age. Maturation age uncertain.
4¾?: Mature at 4¾ years of age. Maturation age uncertain.

respectively, at 10.5 months of age. Their uterine tracts were not turgid. This might indicate that females which are in heat in their first year of life (¾-years-old), tend to come into heat at the very end of the season.

Some females of older age classes have been labelled “Age of sexual maturation uncertain”. The reason for this is that lutein bodies of more than 2 seasons of heat have been detected in only 8 cases. One cannot normally determine the whole reproduction history in the ovaries of females that have experienced more than two mating seasons.

Conclusion: The above-outlined results thus indicate that:

¾-year-old females (7.5–11.5 months): approximately 50 % fertile.

1¾-year-old females (19.5–23.5 months): normally fertile.

Discussion

Analysis of ovaries

As luteal bodies from three different cycles have been detected in eight cases, and all other mature females who had survived at last two mating seasons showed luteal bodies from two cycles, the obtained result is not divergent from findings in related species. Luteal bodies of bobcats *Lynx rufus* last the lifetime of the female (Crowe 1975). Saunders (1961) found luteal bodies from two cycles in the Canada lynx. Luteal bodies from different cycles were determined by methods similar to those employed in the present investigation. Luteal bodies in domestic cats persist for 6 to 8 months after mating (Dawson 1946).

Ovulation rates were stable in different age classes and in different years over a period of 17 years. This is not in correspondence with the results obtained by Brand and Keith (1979) concerning the Canada lynx of Alberta, which showed obvious cycles correlated to prey abundance. The reason for this difference may be a tendency in the European lynx for

prey switching in correspondence with availability of different prey species. A similar tendency has not been found in the Canada lynx, which specializes on the snowshoe hare *Lepus americanus*. This phenomenon is discussed in more detail by Kvam (1990).

Ageing of embryos

Based on near kinship between the European lynx and the Canada lynx it appears reasonable to compare results from Saunders (1961) for ageing the embryos. Ovaries of pregnant Canada lynx females examined by Saunders were histologically in good condition, allowing comparison of lutein bodies with published data on the development of lutein bodies in the domestic cat. The relationship between development of lutein bodies and size of embryos in the domestic cat and Canada lynx was very similar for early stages of gestation. Since the cat embryos were of known age, Saunders (1961) aged his embryos from Canada lynx by comparing crown-rump lengths and weights with data on the cat embryos. As support he refers to embryos in smaller- and larger-sized breeds of dogs, which do not usually differ in size until 40 days of a normal gestation period of 60–63 days. These assumption might support the hypothesis that embryonic development in the European lynx is also parallel to development of cat embryos in early stages of gestation, with the necessary reservation that two different species are compared in this case.

Lindemann (1955) reported birth weight of 69 g and 200 % wight gain from birth to 10 days of age in seven European lynx kittens from Poland raised in captivity. Kittens of two almost fully developed litters of the present material weighed from 268 g to 356 g. According to Lindemann (1955) lynx kittens should be 20 days old before reaching such weights. The present results correspond more closely with Hucht-Ciorga (1988), who reported body weights in European lynx kittens from the Wuppertal zoo, West-Germany: 600 g at 8 days of age indicates a birth weight of approximately 200–300 g, assuming a 200 % weight gain after birth.

Litter size

Lindemann (1956) reported 1–4 kittens with a mode of 2 in Eastern Europe. Ognev (1935) reported 2–3 kittens as normal in the Soviet Union. Satunin (1915) reported a maximum litter size of 3 in Caucasus. Yablonski (1905) considered a litter size of 4 as unusual. He reported in old Siberian hunter to have observed a litter of 5 on one occasion. Saunders (1961) reported a mean litter size of 2.92, with a mode of 3 in Canada lynx from Newfoundland. Valverde (1957) reported a mean litter size of 2.5 with a mode of 2 in Spanish lynx *Lynx pardina*. The range was 1–4. The mean litter size of 2.50 ± SD 0.53 found in the present investigations is in keeping with the values obtained in other studies.

Gestation period

Lindemann (1956) stated a gestation period of 70–72 days in lynx from Eastern Europe. Palmgren (1920) reported parturition on 20–23 May at Högholmen Zoological Garden, Helsinki, Finland. As mating occurred on March 6, this indicates the gestation to have lasted 75–78 days. Ognev (1935) quoting older sources, reported 63–70 days gestation in European lynx of the Soviet Union. Zuckerman (1952) calculated 63 days for captive lynx at London Zoo. Stefan Jonsson (pers. comm.) states a gestation period of 65–70 days in his captive lynx at Tovetorp, Sweden. Based on these sources one might suppose a normal gestation period in European lynx of approximately 70 days. Some variation has to be expected, and one cannot be sure to have observed the very first copulation of a mating period in captive animals.

Mating period

According to VALVERDE (1957) and DELIBES et al. (1975) mating in the Spanish lynx takes place in January and February. WERNER (1953) reported mating during late February in European lynx from the Carpatians and Tatra mountains of Central Europe, while OGNEV (1935) reported March and early April as the normal mating period by lynx in central parts of the Soviet Union. In Caucasus mating is reported to take place in the same period or somewhat earlier. HAGLUND (1966) holds March as the normal mating period in European lynx from Northern Sweden. STEFAN JONSSON (pers. comm.) observed behaviour reflecting "heat" in captive lynx at Tovetorp, central Sweden in the period 25 February–8 April. This information might suggest a delay of the mating period with higher latitude. CROWE (1975) reported a similar pattern in the bobcat.

BIRKELAND (1971) claimed that mating in European lynx from Norway occurs from January 15 through April 15. This investigation supports BIRKELAND's results, indicating a peak of mating activity in March. HAGLUND (1966) suggested a mating period of approximately one month. According to EWER (1973) prolonged mating period is widespread in carnivores. One possible reason for this may be that strong, well armed and solitary living mates may require a certain time to calm down the aggression that close body contact would bring about outside the mating period.

Polyestrous status, and induced ovulation (ASDELL 1946, 1966; EWER 1973) are adaptations that would fit well with the solitary habits of the European lynx. No examined felid species has proved to be monoestrous (EWER 1973). The European lynx may therefore also be polyestrous, since the mating period is so prolonged. The present results do not, however, indicate the European lynx to be truly polyestrous and have more than one ovulation wave per season, as reported for the bobcat, which is also supposed to be a spontaneous ovulator (CROWE 1975). The ovulation rate of the 8 pregnant specimens of the present material corresponds very accurately with observed litter size. Also the low number of fresh corpora lutea and corpora lutea of previous cycles in specimens in their 1st and 2nd year of life indicate no more than one ovulation wave per season. The above outlined pattern fits well with a system of monoestrous status and induced ovulation. But as PERRY (1972) points out, there may not be a clear demarcation between spontaneous and induced ovulators in many cases. Just as spontaneous ovulation may sometimes occur in a species that normally ovulates only after coitus, the converse may be true in that coitus may induce or hasten ovulation in a species that normally ovulates spontaneously.

Parturition date

May 15 was employed as a normal parturition date in age determination of the present material, due to information published by LINDEMANN (1956). ZUCKERMANN (1952) reported birth on May 10 in the London Zoo, and PALMGREN (1920) reported May 20–23 in Högholmen Zoo, Helsinki, Finland. HAGLUND (1966) mentioned a lynx litter observed on May 21. The kittens were estimated to be 12 days old, which means that parturition occurred on May 9. COLLETT (1912) supposed normal parturition in May or June, in some instances even later. Supposed occasional late parturition is reported based on observations of two litters of approximately two weeks of age on 2 and 15 July. The results obtainded in the present study concerning parturition period are in good correspondence with recent data from Tovetorp and Grimsö research stations of Sweden, where the following parturition dates are reported for captive lynxes: 1974: 26 May; 1976: 23 May, 3 June, 6 June; 1977: 18 May, 6 June, 18 June; 1978: 15 May (STEFAN JONSSON, pers. comm.). Since the mating period is rather prolonged and tends to be delayed with higher latitude, parturition will also vary accordingly.

Sexual maturation

LINDEMANN (1955) reported sexual maturation in male European lynx at 33 months or nearly 3 years of age. HAGLUND (1966) and BIRKELAND (1971) quote LINDEMANN without further comments. SAUNDERS (1961) reported male Canada lynx to be sexually immature in their first year of life. His material gave no reliable data on age of maturation. The present investigation demonstrates maturation at 2¾ years of age as a general rule. The results indicate maturation in approximately 50 % of the 1¾-year-old males. But more testes in histologically acceptable condition from this age class will be necessary to draw any definitive conclusions concerning maturation in 1¾-year-old males. According to WERNER (1953) female lynx aggregate at certain mating grounds to court one large older male. Younger males gather around and fight for those females which are chased away by more dominant females. YABLONSKI (1905, quoted OGNEV 1935), who studied the lynx of the Altai mountains in Siberia, reported males chasing the females and fighting for them. This is in correspondence with well known domestic feline habits. Any of these mating systems would lead to low probability for 1¾-year-old mature males to take part in mating. They would most likely be chased away by stronger 2¾-year-old males. The result would be normal mating from 2¾ years of age because of behavioural, and not only physiological reasons.

LINDEMANN (1955) reported sexual maturity in captive female European lynx at 21 months of age. HAGLUND (1966) quoted LINDEMANN without further comment. SAUNDERS (1961) gave the same maturation age in female Canada lynx from Newfoundland. This is in correspondence with results obtained in the present investigation concerning the general rule. However, the present study also indicates maturition in some females in their 1st year of life. Although ovulation in the European lynx may be assumed to be induced by coitus, as in the domestic cat (ASDELL 1946, 1966), lutein bodies do not necessarily imply pregnancy. According to GREULICH (1934) ovulation in domestic cats can be caused artificially by means of a glass rod. This indicates that attempted mating or playing might induce ovulatiion. As a consequence, ¾-year-old sexually mature females, as established by ovary inspection, might not necessarily take full part in reproduction, although they display luteal bodies of recent ovulations. Should they participate and conceive, there is considerable reason to question their ability to raise their young, which would be born shortly after the mother has become able to kill prey and feed herself (JONNSON 1978, 1986).

Acknowledgement

I am indebted to Mr. STEFAN JONNSON for his valuable information on reproduction in captive lynx in Sweden.

Zusammenfassung

Fortpflanzung beim europäischen Luchs, Lynx lynx

Untersucht wurden die fixierten Gonaden von 325 in den Jahren 1960–1976 in Norwegen gesammelten Luchsen. Danach dauert die Paarungszeit von Februar bis Anfang April und hat ihren Höhepunkt im März. Die Jungen werden von Ende Mai bis Anfang Juni geboren. Die Wurfgröße beträgt gewöhnlich 2–3. Die Männchen erreichen meist im Alter von 2¾ Jahren die Geschlechtsreife, einige schon mit 2¾ Jahren. Die Weibchen sind mit 1¾ Jahren fortpflanzungsfähig, Anzeichen für eine Geschlechtsreife bereits im Alter von ¾ Jahren fanden sich bereits bei etwa 50 % der Weibchen.

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Hiding behaviour in wild Gerenuk (*Litocranius walleri*) fawns

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Abstract

Studied the hiding behaviour of wild gerenuk fawns as one important aspect of early development and ecological adaptation. Hiding changes gradually to the anti-predator strategy of the adults and ceases by month 4. Bushes and small trees serve as day hiding sites; night hiding is in heaps of dry branches. Nursing is twice per 24 hrs, and fawns change hiding sites after each nursing period. Both mother and fawn show extraordinary site fidelity; behavioural mechanisms allow for reunion after voluntary or enforced separation. Only during the first 3 weeks of the hiding phase do mothers consume the entire feces and urine of their offspring. Subsequently the fawns defecate and urinate on their own, outside their hiding sites. The investigation was carried out in Samburu National Reserve, Kenya, in 1984 and 1985, and is based on the life histories of 17 females and their 30 known age fawns, all individually identifiable.

Introduction

Although mother-infant behaviour and behavioural development are decisive for a species' ecological adaptation, these aspects have been largely neglected in field studies of African bovids, the exceptions being investigations on hartebeest, *Alcelaphus buselaphus,* (Gosling 1969), bontebok, *Damaliscus dorcas,* (David 1975), Grant's gazelle, *Gazella granti* (Walther 1965) and giraffe, *Giraffa camelopardalis,* (Pratt and Anderson 1979). The aim of this work was to investigate and analyse the mother-young relationship, behavioural development and breeding ecology of wild gerenuk.

Gerenuk inhabit semi-arid thorn bush savanna from Eritrea to northern Tanzania; the western limit is the Rift Valley (Halthenorth and Diller 1977). Gerenuk are browsers. Females live in groups of 5–10 within confined areas of 1–2 km^2, which are congruent with one male's territory (Räder 1982). Unattended young show hiding behaviour and reproduction is throughout the year (Reif 1987).

Material and methods

The investigation was carried out from April 1984 to December 1985 in the Samburu National Reserve, Kenya, (0°34 'N, 37 °E). The study area of 7 km^2 was chosen for its high density of gerenuk, 10–12 per km^2 (as opposed to for example 0.56 per km^2 in Tsavo N.P., Kenya, Leuthold 1978), the habituation of the animals to vehicles and for being motorable.

There are two rainy seasons (October–December and March–April) with an average annual rainfall of 454 mm over the last 25 years (Meteorological Department, Nairobi).

An aerial photograph (scale 1: 11 000, Survey of Kenya, dated 30. 1. 1967) with grids of 110 × 110 and 37 × 37 m was used for mapping.

Observations were made from a Landrover using binoculars 9 × 63 and a telescope 30 × 75. Olympus SLR cameras with 70–210 mm Vivitar and 600 mm Novoflex telelenses were used for photodocumentation. Adults and subadults could be recognised by natural marks: differences in the coat pattern, cuts in the ears, scars on the body and hairless spots. Fawns were identified through their mothers.

The results are based on the observation of 17 adult females and their 30 fawns, whose birthdays

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were known. Only 3 fawns survived to weaning (at age 7–8 months; mortality rate in the first 3 months: 70.7 %).

Data on hiding sites and hiding behaviour were collected by direct observation. Activity patterns and movements were assessed by observing mother-young units continuously from sunrise to sunset and taking the relevant data at 5 min intervals.

Results

Duration of hiding and behaviour in the hiding place

In the first 4 weeks of life gerenuk fawns, except for the two nursing periods, stay on average 9–9.5 hrs hidden and separated from their mothers during the day. The mothers feed and rest out of sight, up to 1.5 km away. Nursing from day 2 until weaning is from 0700–0900 (82.7 %; n = 99) and from 1700–1900 (91.8 %; n = 110). In their day hiding sites 2–21 days old fawns spend on average 90 % of their time lying (n = 7, δ_{n-1} = 4.7 %), 25.4 % thereof with closed eyes. Every ½ to 2 hrs they stand for 1–15 min and stretch. Occasionally they chew dry grass, dark or other objects and rarely they autogroom.

Subsequently day hiding time decreases steadily (Figs. 1, 2): In month 2 the fawns still lie hidden at least 5 hrs during the day; in month 3, day hiding behaviour gradually changes

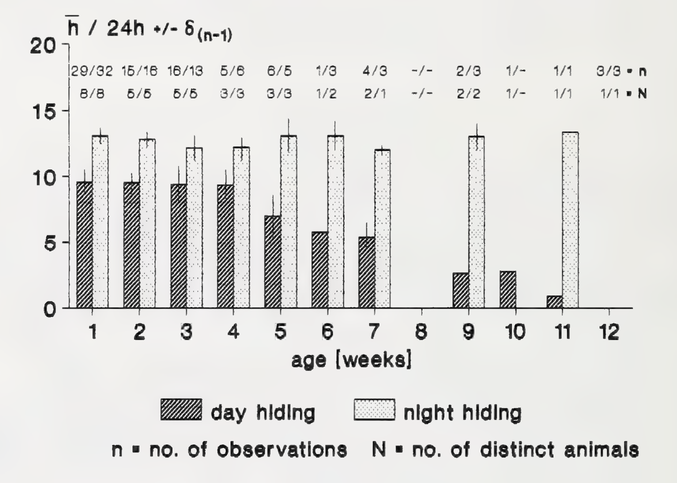


Fig. 1. Average hiding duration (h̄) in 24 h

to the resting behaviour of the adults (Fig. 2). The duration of night hiding in the first 3 months, on average 12–13 hrs, does not change significantly (Fig. 1). Although night observations were not feasible, it can be assumed that fawns which, in the early morning, lay in exactly the same spot that they had lain down in the evening before (n = 106 = 100 %), had actually stayed there throughout the night. At the end of month 3/beginning of month 4 the fawns lie down alone between 1800 and 1900 as before, but at dawn are found feeding or resting somewhere else (n = 15 = 100 %), either alone, with conspecifics or their mothers. From age 5 months, fawns stay with their mothers at least until complete darkness (n = 33 = 100 %).

Beginning and end of a hiding phase, selection of sites

The beginning of a hiding phase is decided by the fawn (n = 229). It separates from the mother and approaches a possible hiding site in a determined manner, sniffing at leaves,

branches, soil and so on. A fawn may check several localities before accepting one, and always paws the ground with its front hooves several times before lying down. In the first week the selection might be influenced by the mother. She may lead her young to a potential hiding site, stand right beside it and repeatedly make contact sounds. The young then lies down in the hiding place selected by the mother (n = 3/75). If a young of this age has chosen a hiding place by itself and the mother gets disturbed in the vicinity, she walks back to the site, calls her young and leads it away (n = 19/75). If the fawn does not get up immediately, the mother repeats the contact sounds and paws the ground with her hooves, in one case even for 15 min, to rouse the fawn.

In the first 6–8 weeks the end of a hiding phase is decided by the mother, who arrives near the hiding site at nursing times and displays special behaviour sequences. In sight of the hiding place, she looks at it, walks determinedly towards it, stopping and sniffing every 15–20 m for 10 sec to 1 min, alert and with head erect. When within 15–20 m she stands still and in an erect position, facing the young and calls. The fawn then walks or runs to the mother. After age 6–8 weeks the fawns end the day hiding phase independently, whereas the end of night hiding is decided by the mother until the age of about 11 weeks.

Characteristics of hiding sites

Day and night hiding sites differ considerably in their characteristics. For a day hiding place gerenuk fawns always select green or dry bushes and small, partly bushy trees (n = 123; Tab. 1). During the dry seasons fawns lie right in these bushes (Fig. 3a). In the rainy seasons, when grass and herbs are abundant, prefered sites are in high ground vegetation at the edge of a bush (85.4 %; n = 48; Fig. 3b). If later on in the day the place is exposed to the sun the fawn moves to another one, 2–15 m away. At night fawns up to age 9–10 weeks select dead branches (79.3 %) and dry grass whisks (17.0 %) for hiding sites (n = 106; Tab. 2). In dry seasons they hide between the branches (Fig. 3c), during the rains they prefer sites next to dead wood in high ground vegetation. From age 9–10 weeks the quality of night hiding places changes and the fawns lie in high grass near small bushes, or just on open grass patches like adults (n = 15).

Use of sites

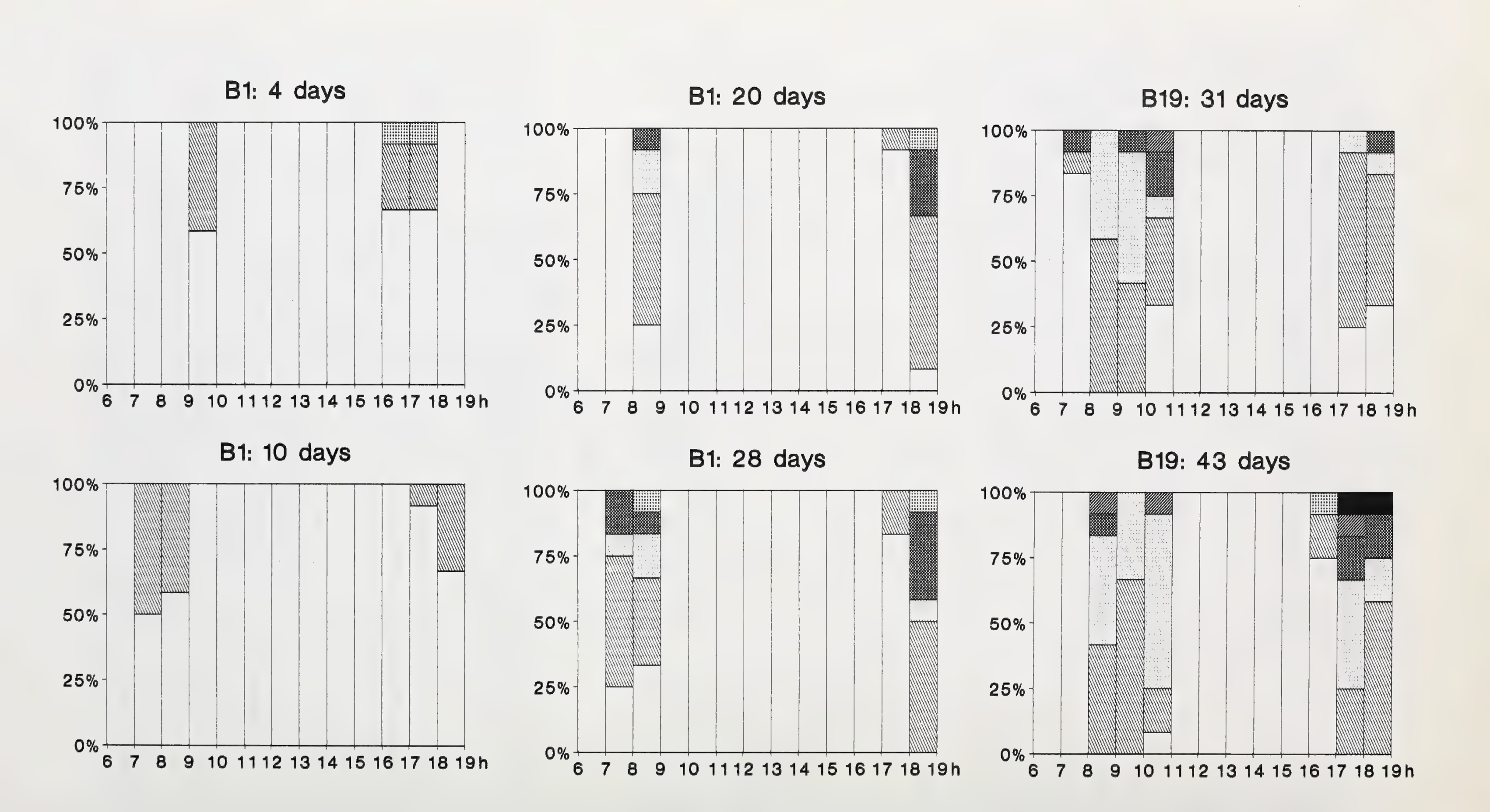
A day hiding site is never used for the night nor vice versa, but sites may be used repeatedly. 12 fawns of ages 2–77 days used on average 24 % of their hiding sites more than once (n = 258). If at hiding time a fawn is in the vicinity of a previously used hiding place, it will usually walk or run straight towards it, occasionally taking cover, and immediately lie down when reaching it. In order to reach a previously used hiding site fawns aged 2–4 weeks frequently covered distances of 25–40 m, rarely up to 100 m, those of 4–5 weeks often 100 m, but even up to 400 m.

From age 9–10 weeks, young using open sites at night may do so several times, for examples 7 out of 12 nights (observations spaced irregularly from fawn age 76–145 days).

Spacing of hiding sites and movements

On all observed occasions (n = 13) the mother led the newborn 100–400 m to the first hiding site within 1–3 hours after birth. Most mothers (n = 11/13) then left their fawns and stayed in the vicinity up to 100 m away, but had no further physical contact with them until the evening nursing session. Some mothers (n = 2/13) repeatedly came back to the hiding sites, roused their fawns, nursed them and led them to new hiding places. One of them roused her newborn 4 times in the first 8 hours.

Subsequently, the pattern is quite uniform. In the first and part of the second week of


B1: 4 days
B1: 20 days
B19: 31 days
B1: 10 days
B1: 28 days
B19: 43 days
100%
75%
50%
25%
0%
6 7 8 9 10 11 12 13 14 15 16 17 18 19h

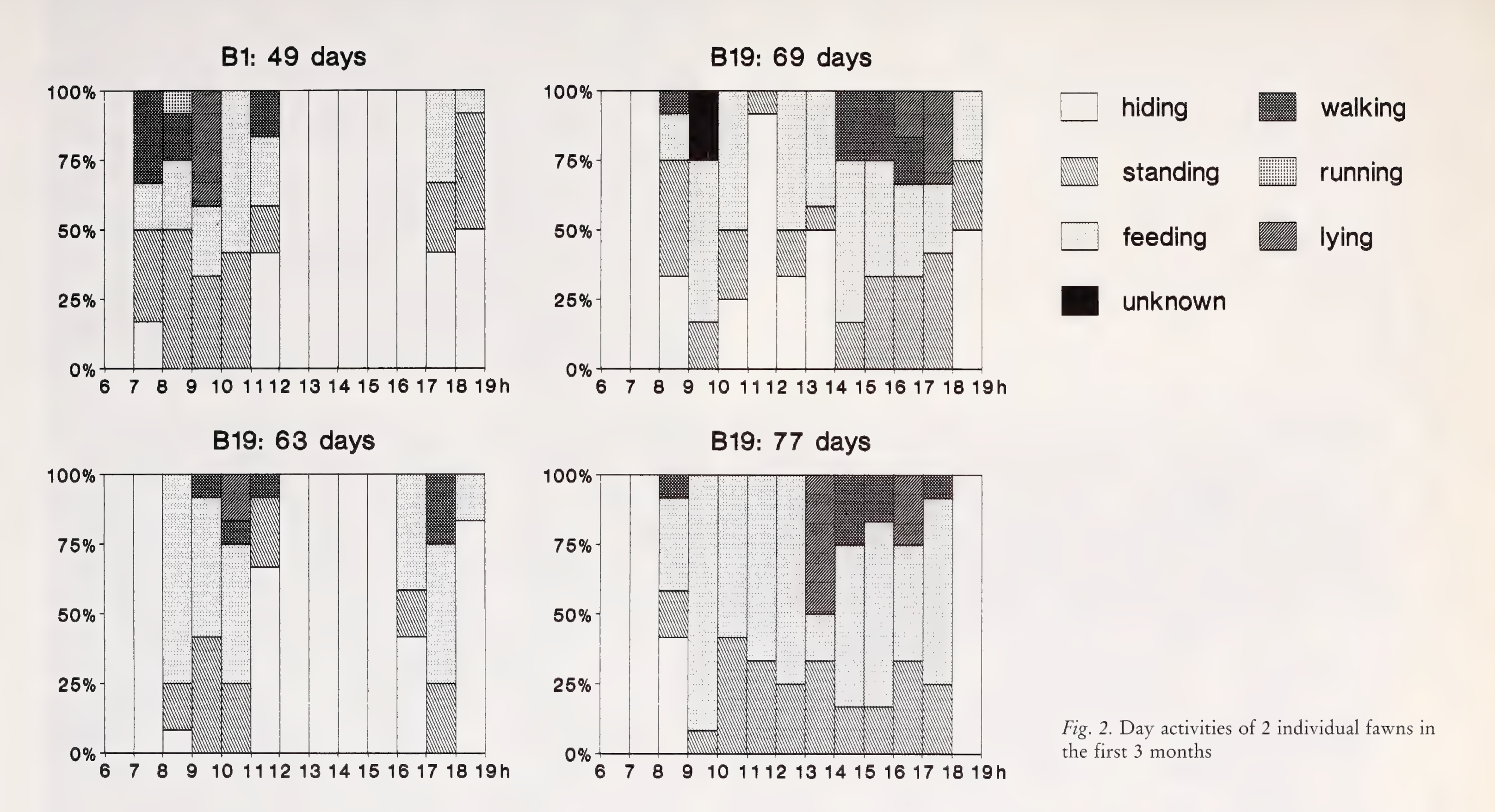


Fig. 2. Day activities of 2 individual fawns in the first 3 months

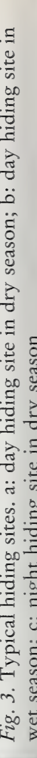


Fig. 3. Typical hiding sites. a: day hiding site in dry season; b: day hiding site in wet season; c: night hiding site in dry season

Table 1. **Specification and relative frequencies of day hiding sites**

Specification of hiding site	Dry season n = 75; (%)	Wet season n = 48; (%)
Acacia reficiens	20.0	–
Acacia senegal	10.6	2.1
*Acacia tortilis**	9.3	16.7
Boscia coriacea	–	2.1
Bush group (green)	–	14.6
Commiphora spec.	8.0	12.5
Combretum aculeatum	–	4.2
Grewia spec.	5.4	39.6
Maerua spec.[1]	6.7	6.3
Salsola dendroides[1]	2.7	–
Salvadora persica[1]	13.3	2.1
unidentified dry bushes	24.0	–

[1] evergreen; others are deciduous.

Table 2. **Specification and relative frequencies of night hiding sites**

Specification of hiding site	Dry season n = 63; (%)	Wet season n = 43; (%)
Dead wood with grass	–	53.5
Dead wood without grass	82.5	20.9
Dry, high grass whisks	14.2	20.9
Stones	3.1	–
Green bush	–	4.7

life the fawn uses day and night hiding sites in an area of 2.4–5.6 ha, and mother and fawn, if not disturbed, stay in this area for the nursing periods (n = 71; N = 6; mean = 3.9 ha, δ_{n-1} = 1.2 ha). In the following weeks the mother enlarges her fawn's range by moving about with it during nursing periods. Consequently, successive hiding places are spaced further apart. At age 8–10 weeks the fawn's range is the same as its mother's.

Fidelity to sites

Gerenuk mothers and fawns demonstrate great familiarity with their home range. No matter how far away a mother is from the hiding place of her young (up to 1.5 km) or in which direction she had fled when disturbed while nursing, she always returns in a straight line. If a fawn has changed sites, the mother calls repeatedly and circles the spot where they were last together. The fawn in turn walks slowly towards the place of separation. In this way mother and young reunite. Mutual searching occurs exclusively at nursing time. After the death of an offspring the mother searches for her fawn at the place of last contact for 2–3 consecutive nursing periods (n = 22).

Defecation and urination

Gerenuk fawns defecate and urinate only outside their hiding sites. For the first weeks of life defecation and urination is assisted by the mother. During or immediately after suckling, the mother licks the genital and anal regions of her young and consumes its feces and urine. The average frequency of this nursing behaviour (Fig. 4) drops considerably in

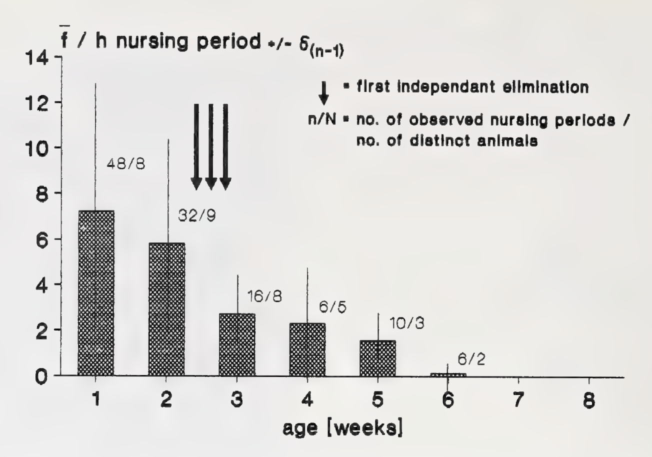


Fig. 4. Average frequency (f̄) of mother assisted elimination per hour (h) nursing period

week 3 and ceases by week 6. The first bout of feces and urine intake by the mother lasts 1–2, in some cases up to 3 min; later bouts in the same nursing period last between 5 and 30 sec.

The change from mother assisted to independent elimination is gradual. At age 18–21 days (Fig. 4) the fawns attempt to defecate on their own for the first time, displaying for 1–5 min the typical stance with tail streched out, producing not more than one pellet, often none at all. At the same time they start urinating on their own. From age 6–7 weeks the fawns defecate and urinate like adults.

Discussion

In terms of mother-infant relationships, Walther (1965, 1966, 1968) distinguishes "Followers" and "Hiders". Following behaviour is the adequate anti-predator strategy in open habitats (Lent 1974; Estes 1976) and is often associated with migratory habits. In forest and bush habitats the typical strategy is hiding whose efficiency is enhanced by (a) the young changing hiding sites after every nursing period, (b) the mother avoiding leaving her scent at the hiding place, (c) the mother consuming the fawn's eliminations and thereby preventing olfactory cues (Lent 1974). Hiding also saves energy and water (Langman 1977).

Although hiding behaviour of several bovid species has been observed in zoos and in the wild (overview Walther 1979), data on age-related changes in daily hiding time are only available for captive greater kudu, *Tragelaphus strepsiceros* by (Walther 1964). This study presents the first detailed data on this subject for a wild bovid.

The hiding period of gerenuk can be divided into 3 phases:

1. Consistent day and night periods during month 1.
2. Gradual decrease in the duration of day hiding in months 2 and 3 until it vanishes completely. Change of characteristics of night sites during month 3.
3. Progressively shorter night hiding periods during month 4, until they cease altogether.

The first changes in the pattern of hiding are during the day, with fawns becoming active on their own in the early afternoon when predator activity is low. At nursing time in the evening, when predators are more active, the fawns reunite with their mothers. Changes in the night hiding pattern occur only 4–6 weeks later.

The changing of hiding sites after every nursing period as in gerenuk has also been described for reedbuck (Jungius 1970) and Grant's gazelle (Walther 1965). The selection

of qualitatively different day and night hiding sites has so far not been observed in other species, however WALTHER (1968), noted the selection of different localities for day and night hiding in captive sitatunga fawns, *Tragelaphus spekei.*

Bushy day hiding places provide shade and visual screening from diurnal avian and terrestrial predators (Martial eagle, *Polemaetus bellicosus,* Verraux's eagle, *Aquila verreauxi,* cheetah, *Acinonys jubatus,* and wild dog, *Lycaon pictus*). However, the dry wood and grass characteristic of night hiding sites – which would crackle if touched – may provide an audible form of protection from nocturnal predators. Predators hunting at night most probably try to avoid making such noises. Also it was noted that carnivores like wild cat (*Felis silvestris*), bat-eared fox (*Otocyon megalotis*) jackal (*Canis mesomelas*) and leopard (*Panthera pardus*), often were found lying in bushes considered to be suitable day hiding places for gerenuk fawns. Therefore use of a day hiding place at night might carry the risk of being discovered accidentally in the early morning by a retiring predator. This may be important, if one remembers that gerenuk mothers do not guard the hiding places of the young permanently as in the Grant's gazelle (WALTHER 1965).

The consumption of the fawn's feces and urine by the mother has been documented in other bovids of the hider type, such as Grant's gazelle, *Gazella granti* and other gazelles (WALTHER 1966, 1968), waterbuck, *Kobus ellipsiprymnus* (SPINAGE 1969), lesser kudu, *Tragelaphus imberis* (LEUTHOLD 1979), hartebeest, *Alcelaphus buselaphus* (GOSLING 1969), and reedbuck, *Redunca arundinum* (JUNGIUS 1970). To what extent this behaviour acutally does protect the young as claimed by some authors (for example GOSLING 1968), is difficult to assess. Hiding roe deer fawns (*Capreolus capreolus*), for example, are easily roused by dogs (BUBENIK 1965). In this study also it was determined from tracks that a leopard roused a 10 days old gerenuk from its night hiding place by following its spoor to the hiding site, but failed to make a kill. Supposing that the intake of feces and urine by the mother minimises scent cues as to the whereabouts of the fawn, the questions arise as to why this behaviour is not displayed throughout the entire hiding phase, and why it is not correlated with changes in the hiding pattern. However, the fact that in gerenuk the first independent elimination of feces and urine coincides with the first intake of plant matter (Fig. 2) and with a marked decrease in mother assisted elimination (Fig. 4), indicates a causal relationship between the fecal composition of the fawn and mother assisted elimination.

The possibility that the eliminations of fawns – while they are subsisting on milk – could be a valuable additional source of nutrients for the mother has so far not been discussed. Furthermore, the fact that fawns keep their hiding places clean even after they defecate and urinate idependently would seem to be equally important as an antipredator strategy as the intake of the eliminations by the mother.

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Zusammenfassung

Abliegeverhalten bei Gerenuk-Kitzen (Litocranius walleri)

Das Abliegeverhalten des Gerenuks ist eine Feindvermeidungsstrategie, die an die unterschiedlichen Such- und Jagdmethoden von Tag- bzw. Nachtfeinden angepaßt ist. Tag-Abliegeplätze befinden sich an bzw. unter Büschen und kleinen Bäumen, Nacht-Abliegeplätze in trockenem Fallholz.

Im ersten Lebensmonat sind Gerenuks streng Ablieger. Danach nimmt die Abliegezeit allmählich ab und das Aktivitätsverhalten geht im 4. Monat in das der Erwachsenen über.

Nach jedem Säugen, 2mal in 24 Stunden, wechseln die Kitze den Abliegeplatz. Abliegeplätze werden auch mehrfach verwendet.

Mutter und Kind zeigen extreme Ortstreue und Ortskenntnis, die ihnen das Wiederfinden nach freiwilliger oder erzwungener Trennung ermöglichen.

Mütter nehmen Kot und Harn ihrer Jungen in den ersten 3 Wochen vollständig auf. Danach koten und harnen die Kitze zunehmend selbständig, immer aber außerhalb ihrer Abliegeplätze.

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Genetic study of Sand gazelles (*Gazella subgutturosa marica*) from Saudi Arabia

Chromosomal and isozymic data

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Abstract

Presented the karyotype and electrophoretic variability at 20 loci of captive sand gazelles (*Gazella subgutturosa marica*) from Saudi Arabia. The most commonly encountered diploid numbers were 33 chromosomes for the males and 32 for the females, due to an X-to-autosome translocation commonly reported in the tribe Antilopini. Nevertheless, 4 females displayed diploid numbers of 31 chromosomes caused by a centric Robertsonian fusion in an heterozygous form. This probably results from previous hybridization with the subspecies *G. s. subgutturosa.* Percentage of polymorphic loci and mean heterozygosity were 15 % and 0.017, respectively. This latter quite low value, as well as the chromosomal polymorphism observed, may be due to previous lack of genetic management when this captive herd was founded. Nevertheless, the fact that some genetic variability remains in this endangered subspecies is encouraging in the perspective of its reintroduction in the wild, providing that the distribution of the chromosomal fusion and its possible consequences on reproduction and survival are checked.

Introduction

There is an urgent need for protection measures and establishment of captive-breeding programs for a number of species of gazelles (genus *Gazella*) that are seriously threatened today (Ryder 1987; Groves 1988). In this respect, one must know as precisely as possible the genetic status of the groups studied, both for breeding management purposes (Wayne et al. 1986; Templeton 1986) and for optimization of reintroduction plans (Allendorf 1986; Allendorf and Leary 1986).

In the present paper, we describe the genetic variability based on electrophoretic and karyologic results in a sample of *Gazella subgutturosa* from Saudi Arabia. The Goitred gazelle, or "rheem" *G. subgutturosa* is one of the three gazelle species native to Saudi Arabia (Thouless et al. 1991), where it is represented by the subspecies *G. subgutturosa marica,* the Sand gazelle (Harrison 1968). Although less threatened than the two other species (*G. gazella* and *G. [dorcas] saudiya*), the Sand gazelle has become rare in Saudi Arabia, and a captive-breeding program initiated by the National Commission for Wildlife Conservation and Development (NCWCD) has started in order to reintroduce the species into the wild (Thouless et al. 1991). Several hundreds of Sand gazelles are thus bred in Saudi Arabia, which are thought to represent a pure sample of the Arabian peninsula subspecies *G. subgutturosa marica,* according to external and skull morphology (Al Basri and Thouless, unpubl. data).

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Material and methods

Origin of the animals

The individuals studied originate from animals captured in the wild in different regions of Saudi Arabia (but precise locations are not known) between 1976 and 1982 and then bred near Riyadh in Prince Khaled farm, which became the King Khaled Wildlife Research Center (KKWRC) in 1986. Unfortunately, no details upon the numerical evolution of the herd during these first years are available, as no management of any kind was performed. At the KKWRC establishment, about 200 rheem were present, a number that has nearly doubled today. From here, a group of 24 animals has been brought into pre-release enclosures in the Mahazat as Saïd Reserve, the first site where reintroduction of the species is planned.

The isozyme survey was performed on 30 individuals, 19 of which belong to the group that is to be released in the Reserve. 23 animals from this latter group were karyotyped, as well as 7 additional individuals which will be reintroduced to the wild later on.

Karyotypes

The karyotypes were established from lymphocyte cell cultures. About 10 ml of peripheral blood were collected aseptically by jugular punction into heparinized sterile glass tubes. Ten drops of blood (0.5 ml) were distributed into vessels containing 9.5 ml of HAM'SF 12 nutritive mixture supplemented with 20 % fetal calf serum, antibiotics (100 UI) and concanavalin A (10 µg/ml). The culture was then incubated at 37 °C for 72 hours, and colcemid (final concentration 0.03 µg/ml) was added one hour before harvesting. The cells were then treated with a hypotonic solution of sodium citrate (0.85 %) for 20 min at 37 °C, fixed with Carnoy's solution, spread on previously cooled slides and stained with a 4 % Giemsa solution. The best metaphases were photographed and karyotypes were then prepared.

Protein electrophoresis

Blood samples were taken by jugular punction and stored in heparinized tubes at 4 °C until treatment. Saline solution was added before the first centrifugation, after which the plasma fraction was separated from the red cells. After several washes in saline solution, the red cell samples were prepared by a hypotonic shock in distilled water. The plasma and red cell samples were then kept at −30 °C until electrophoresis was performed.

Twenty loci were analysed using horizontal starch-gel electrophoresis according to Pasteur et al. (1987) with a starch concentration of 12 %. Staining procedures were according to Pasteur et al.

Table 1. **Enzymes studied, number of loci per enzymes, tissue (RBC = Red Blood Cells) and buffer system used**

(see text)

Enzyme	Loci	Tissu	Buffer
Aspartate-aminotransferase (AAT)	1	RBC	TME6.9/TME6.9
Acid-phosphatase (ACP)	1	RBC	TC6.4/TC6.0
Diaphorase (DIA)	1	RBC	TC6.4/TC6.0
Esterase (EST 10–14)	2	RBC	TME6.9/TME6.9
Glyoloxase (GLO)	1	RBC	TBE8.6/TBE8.6
Glucose 6-Phosphate dehydrogenase (G6PDH)	1	RBC	TME6.9/TME6.9
Glucose phosphate isomerase (GPI)	1	RBC	TC6.4/TC6.0
Lactate dehydrogenase (LDH)	1	RBC	TC6.4/TC6.0
Malate dehydrogenase (MDH)	1	RBC	TC6.4/TC6.0
Malic-enzyme (MOD)	1	RBC	TC6.4/TC6.0
Mannose phosphate isomerase (MPI)	1	RBC	TC6.4/TC6.0
Phosphogluconate dehydrogenase (PGD)	1	RBC	TC6.4/TC6.0
Purine nucleoside phosphorylase (NP)	1	RBC	TME6.9/TME6.9
Superoxyde dismutase (SOD)	1	RBC	TC6.4/TC6.0
Hemoglobin (Hb)	2	RBC	TBE8.6/TBE8.6
Albumin (ALB)	1	Plasma	LiOH8.3/LiOH8.1
Esterase (EST 1)	1	Plasma	LiOH8.3/LiOH8.1
Transferin (TRF)	1	Plasma	LiOH8.3/LiOH8.1

(1987). Table 1 lists the loci and buffers used: Tris-Citrate (TC) pH 6.4 (gel) and 6.0 (electrode); Tris-Maleate-EDTA (TME) pH 6.9; Tris-Borate-EDTA (TBE) pH 8.6 and Tris-Lithium-Citrate-Borate (LiOH) pH 8.3 (gel) and 8.1 (electrode), as described by Pasteur et al. (1987).

Results

Karyotypes

The diploid numbers in the 30 individuals studied were found to be as follows: 2n = 33 in the 11 males (Fig. 1), 2n = 32 in 15 females (Fig. 2) and 2n = 31 in 4 females (Fig. 3). The males have 26 meta-submetacentric, 6 acrocentric and 1 large submetacentric chromosomes. The 2n = 32 females have 26 meta-submetacentric, 4 acrocentric autosomes and 2 large submetacentric X chromosomes. In the 4 females whose diploid number equals 31, one more large metacentric chromosome is found, but there are only two acrocentric chromosomes. This pattern is probably reflecting the presence of a centric Robertsonian fusion in an heterozygous form in these 4 animals.

Protein electrophoresis

Three (Trf, Gpi and Np) of the twenty loci studied were polymorphic in the sample (Tab. 2). This yielded a percentage of polymorphic loci ($P_{99\%}$) of 15 %. Two alleles were found at each of the polymorphic loci, which resulted in a mean number of alleles per locus (A) of

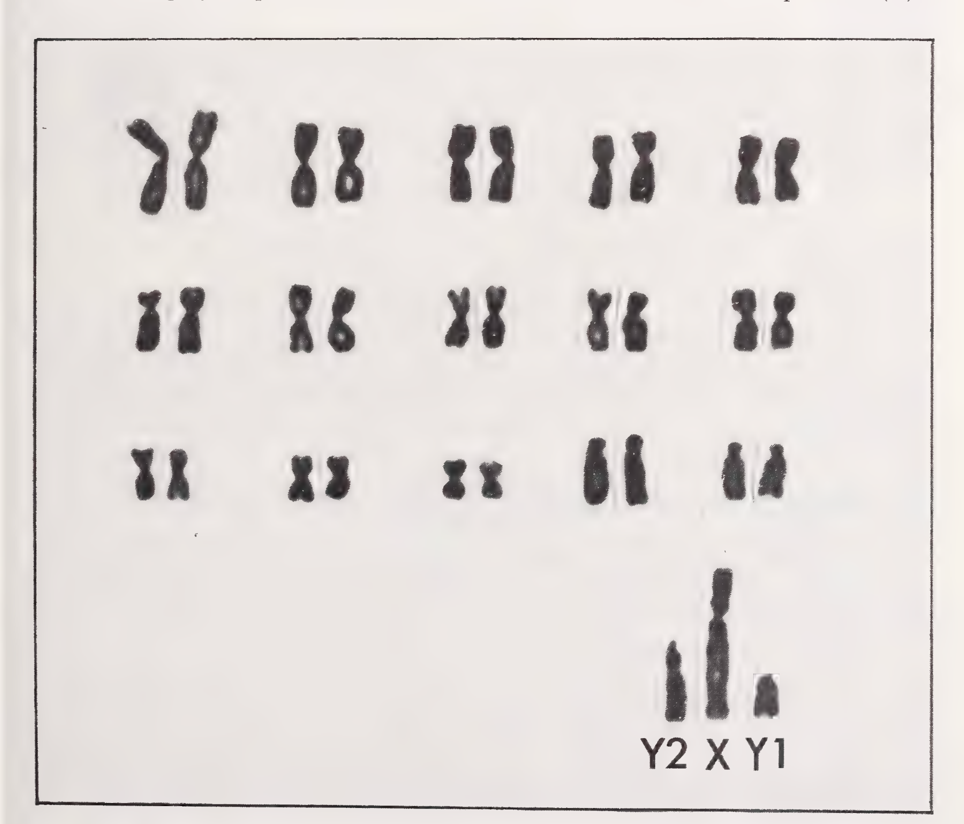


Fig. 1. Karyotype of a male *Gazella subgutturosa marica* with 2n = 33 chromosomes

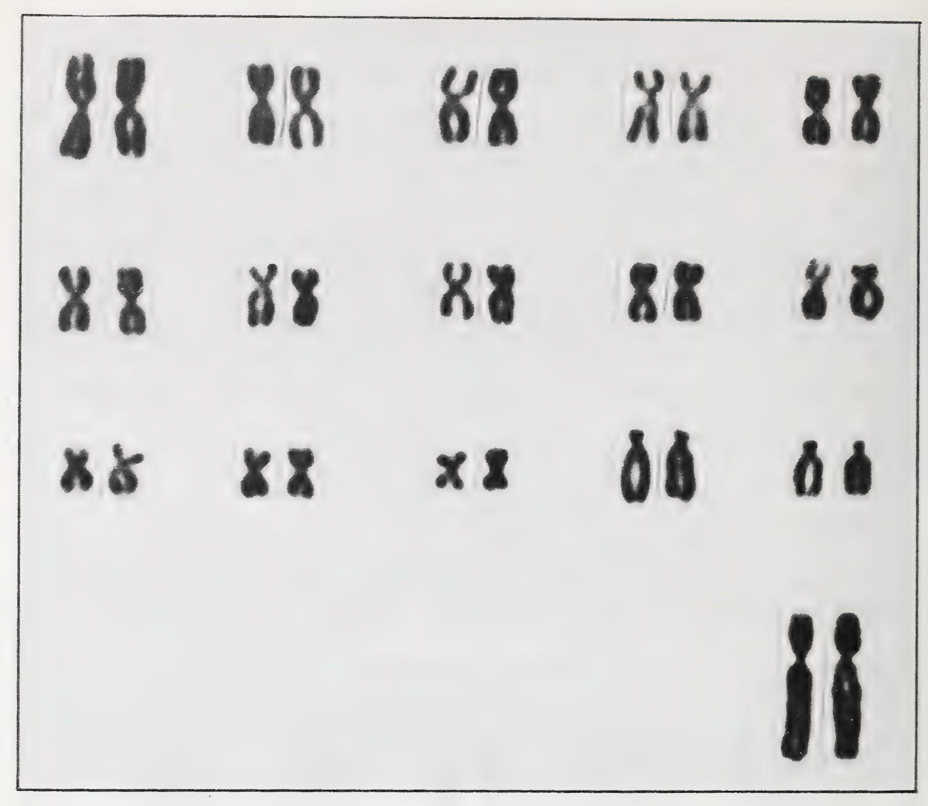


Fig. 2. Karyotype of a female *Gazella subgutturosa marica* with 2n = 32 chromosomes

1.17. From the allelic frequencies, heterozygosity was calculated at each of the three variable loci, and the mean heterozygosity (H) was 0.017 (Tab. 2).

It should be noted that the Trf and Np loci were polymorphic only within the 19 individuals from the Mahazat as Saïd Reserve. When calculated in this group of 19 individuals only, the value of H reaches 0.023. Nevertheless, the absence of the Np^{120} and Trf^{110} alleles in the 11 individuals from the KKWRC probably reflects a sampling effect as these two alleles are in low frequency and would likely be found in a larger group of Sand gazelles from KKWRC.

Table 2. **Allelic frequencies and heterozygosities for the polymorphic loci, and values of P, A and H for the whole sample**

Locus	Alleles	Allelic frequencies	Heterozygosity
Trf	100 110	0.97 0.03	0.064
Gpi	100 120	0.95 0.05	0.095
Np	100 120	0.90 0.10	0.180

Mean heterozygosity H = 0.017; Mean number of alleles per locus A = 1.17; Percentage of polymorphic loci P (99 %) = 15 %.

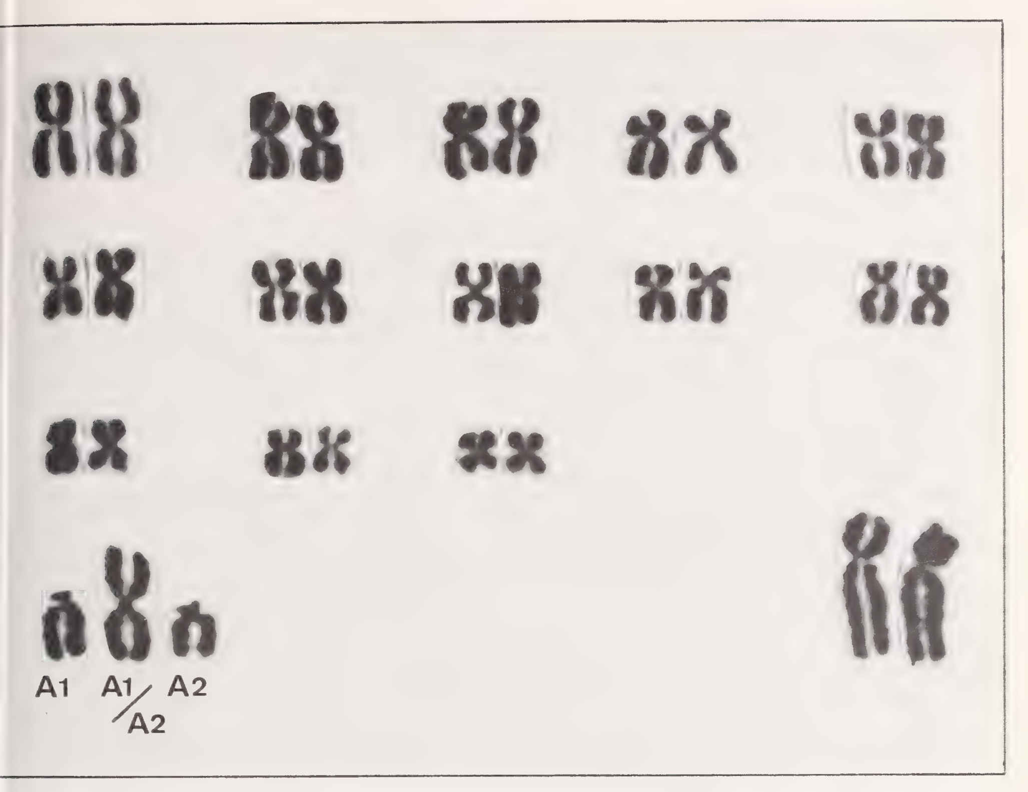


Fig. 3. Karyotype of a female *Gazella subgutturosa marica* with 2n = 31 chromosomes. The large A1/A2 metacentric autosome results from the fusion of two acrocentric ones (A1 and A2)

Discussion

Previously reported karyotypes of other members of the tribe Antilopini have been found to display peculiarities in the sex chromosome morphology. They have an unusually large X chromosome corresponding to an X-to-autosome translocation. Thus, males have one more chromosome (Y2) owing to the translocation of the acrocentric autosome onto the X chromosome (Wurster 1972). This is the case here.

Effron et al. (1976) found in a sample of *G. subgutturosa,* the origin and subspecific rank of which were not specified, a karyotype of 31 chromosomes in 2 males and of 30 in 1 female, with 28 metacentric autosomes. Wurster (1972) found the same result for 3 females studied. The subspecies name was not provided either, but the animals were called Persian gazelles, which is the usual name for *G. subgutturosa subgutturosa.* Diploid numbers of 30 and 31 are also reported for *G. subgutturosa* from China, where only *G. subutturosa subgutturosa* is met (Orlov, in Shi 1987).

In their sample of supposed Sand gazelle (*G. subgutturosa marica*), Kingswood and Kumamoto (1988) found chromosome numbers of 31 (N = 18 individuals), 32 (N = 19) and 33 (N = 1) in males, and 30 (N = 10), 31 (N = 12) and 32 (N = 11) in females. The Persian gazelles (*G. subgutturosa subgutturosa*) they studied have diploid numbers of 31 (N = 5) in males and 30 (N = 4) in females. Based on these data, as well as the fact that there was an exact homology of G-banding patterns between all chromosome pairs of a male

Persian gazelle (2n = 31) and those of a male Sand gazelle (2n = 31), the authors argued the possibility that their Sand gazelle sample may in fact correspond to hybrids between the original stock of Sand gazelles and Persian gazelles, particularly since the origin of the animals sent to the USA was not well known. Moreover, breeding records were found to be different between Sand (or supposedly so) and Persian gazelles, Sand gazelles having less offspring. This fact could effectively result from on outbreeding depression following hybridization between two subspecies.

The results presented here confirm to a certain extent the hypothesis of Kingswood and Kumamoto (1988) concerning Goitred gazelles from the US zoos, as the true diploid numbers for *G. subgutturosa marica* seem to be 33 for males and 32 for females. Nevertheless, we also face the question of a probable introgression phenomenon with *G. subgutturosa subgutturosa* in the Saudi herd, as the 4 females with diploid numbers of 31 are likely to represent hybrids between the two subspecies. This hybridization seems, however, to be much less important than reported in gazelles from the US zoos, as the proportion of hybrids appears to be much lower. Anyway, in both cases morphological descriptions were useless to predict chromosomal findings, as the phenotype *"marica"* (smaller size, paler colour, better-developed horns in females, Harrison 1968) was observed in all specimens, even in those having a true *"subgutturosa"* caryotype (sample of Kingswood and Kumamoto 1988).

So far, we can't discuss the genetic variability of a pure sample of *G. subgutturosa marica.* Even without taking into account the two individuals (one of which has a Trf^{110} allele) with hybrid caryotypes that were included in our electrophoretic survey, we can't rule out the possible integration of Persian gazelles' genes into genomes of individuals chromosomally characterized as Sand gazelles, through recombination. Considering these restrictions, the percentage of polymorphic loci of 15 % observed in our sample is in the range of those found in a number of species of artiodactyles (review in Baccus et al. 1983, and in Vassart et al. in prep.). It is also close to the result of 14 % found by Templeton et al. (1987) in a captive herd of Speke's gazelle. Nevertheless, it appears to be somewhat lower than values obtained in samples of African gazelles *G. dorcas* and *G. thomsoni* (Vassart et al. in prep.). As far as the mean heterozygosity is concerned, the result found here (H = 0.017) is rather low when compared with data from the references cited above. This finding must be stressed, particularly in this case where a reintroduction program is going on, since sufficient heterozygosity is important in short-term success of a species in the wild (Allendorf 1986). This lower heterozygosity rate observed probably results in part from an absence of genetic management of this Sand gazelle herd, at least during a period of low effective size of the breeding group. At that time, genetic drift associated with group structure (see Lacy 1987) may have had important effects on genetic diversity.

Such failures in the management of the herd and in the checking of the animals' origin would also be responsible for the probable hybridization with *G. subgutturosa subgutturosa,* leading to the observed chromosomal polymorphism. The study of natural specimens of both subspecies in their particular range (and especially *G. subgutturosa marica*) is still needed to definitely clarify this situation. As far as the captive-breeding and reintroduction program is concerned, the distribution of the Robertsonian fusion must be precised by an extensive karyological study and its possible consequences on the adults breeding rate and juveniles survival and growth have to be documented (see Kingswood and Kumamoto 1988). Prior to that, it seems preferable to choose only those individuals displaying the 2n = 33 (males)/32 (females) karyotypes for reintroduction into the wild. This selection of individuals should also be achieved in such a way as to maintain as much genetic variability as possible. This last point could be achieved through a screening of the polymorphic loci described here on a larger sample of individuals, as well as through the finding of new variable loci.

Acknowledgements

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Zusammenfassung

Genetische Untersuchungen an Sandgazellen (Gazella subgutturosa marica) aus Saudi-Arabien. Chromosomale and elektrophoretische Daten

Bei in Gefangenschaft nachgezüchteten Sandgazellen (*Gazella subgutturosa marica*) aus Saudi-Arabien wurde der Karyotyp und die elektrophoretische Variabilität in 20 Loci untersucht. Männchen hatten 2n = 33 und Weibchen 2n = 32 Chromosomen infolge der bei den Antilopini häufig beobachteten Translokation des X-Autosoms. Indessen besaßen vier Weibchen 2n = 31 Chromosomen infolge zentrischer Robertsonischer Fusion in einer heterozygoten Form. Dies ist wahrscheinlich auf vorherige Hybridisierung mit der Unterart *G. subgutturosa subgutturosa* zurückzuführen. Der Prozentsatz polymorpher Loci sowie die mittlere Heterozygotierate beliefen sich auf 15 % beziehungsweise 0.017. Dieser letzte, ziemlich niedrige Wert sowie der beobachtete chromosomale Polymorphismus mögen auf vorherigen Mangel an genetischer Organisation zur Zeit der Gründung der Herde beruhen. Die Tatsache aber, daß eine gewisse genetische Variabilität in dieser gefährdeten Unterart verbleibt, ist ermutigend in Hinblick auf ihre Wiedereinbürgerung in die freie Wildbahn, vorausgesetzt, daß die Verteilung der chromosomalen Fusion und ihre möglichen Auswirkungen auf Reproduktion und Überleben überprüft werden.

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A morphometric analysis of the skulls of *Xerus inauris* and *Xerus princeps* (Rodentia; Sciuridae)

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Abstract

Studied morphological and morphometrical differences of skulls of *Xerus inauris* and *X. princeps*. Among the qualitative characters, the colour of the incisivi is the best character to differentiate between the two species. Nine more characters turned out to be extremely useful for the identification of the skulls. In fourteen different skull measurements, the condylobasal length, occipitonasal length, interorbital width, postorbital width, nasalia width and incisivi diameter show highly significant differences between the two species. Skulls of *X. inauris* show a tendency to become smaller with narrower nasalia but increasing diameter of the incisivi from the Orange Free State (South Africa) to Namibia.

Introduction

The southern African ground squirrels *Xerus inauris* and *X. princeps* are rather similar in their general appearance: their pelage is cinnamon dorsally with a white lateral stripe and a white and black pattern on the tail. The discriminating characters for the skulls generally used in keys and descriptions (ELLERMAN et al. 1953; AMTMANN 1975; DE GRAAFF 1981; SMITHERS 1983) are the colour of the incisors (white in *X. inauris*, yellow to orange in *X. princeps*) and the orbit (also called diameter of the orbit or eye orbit) in relation to the occipitonasal length (orbit normally rather less than ⅓ of the occipitonasal length in *X. inauris* and normally more than ⅓ of occipitonasal length in *X. princeps*).

While the first discriminating character (colour of the incisivi) allowed identification of the two squirrel species, the second discriminating character (orbit to occipitonasal length) in use so far seemed very unsatisfactory and will be discussed in more detail later in this paper. Until quite recently even their status as different species seemed debatable (GRUBB 1978) and there were doubts whether the skull measurements would withstand a discriminant analysis (DE GRAAFF 1981). Therefore a detailed qualitative and quantitative investigation was initiated, which was coordinated by J. D. SKINNER. The aim of this study was to check and measure a sufficient number of skulls, to elaborate and define the differences, and perform a multivariate linear discriminant analysis to answer the question of their species identity.

Material and methods

Skull morphology and morphometry

Altogether 302 skulls of *X. inauris* and 49 of *X. princeps* were examined. The material belonged to the following museums: Museum Alexander Koenig, Bonn; Kaffrarian Museum, King Williamstown; Museum of Natural History, London; Naturhistorisches Museum Wien, Vienna; State Museum of Namibia, Windhoek; Transvaal Museum, Pretoria.

Only skulls with complete definitive dentition were used to discern between the two species since too few skulls of younger specimens of *X. princeps* were available. Eight qualitative characters were established on the cranium and two on the mandible (Tabl. 1; Fig. 1). The form of the proximal end of the nasal bone, parieto-temporal suture and the shapes of the zygomatic process of the temporal bone

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and the maxillar process in front of the first cheek tooth were also examined but did not differentiate well between the two species and hence are not discussed any further. The characters were critically viewed by the senior author and then categorized as either typical for one of the two species or as intermediate.

The skull measurements taken are listed in Tab. 2 and illustrated in Fig. 2. In a smaller series the "orbit" or "orbital length" according to Moore's (1960) definition (the greatest inside distance from the anterior edge of the orbit, in the notch of the lacrimal bone, to the posterior extremity of the orbit on the edge of the zygomatic process of the squamosal) was also measured.

Data analysis

The main tool of the data analysis was a multivariate linear discriminant analysis. This method produces scores which very efficiently discriminate between the groups under study. These scores are linear combinations of the original characters computed for each group and separate the groups better than any of the characters considered on their own. Before the analysis those characters were excluded which did not show significant differences among groups at the 5 % probability level in an univariate F-test.

The analysis compresses the information contained in the full character set from each individual into canonical scores for various combinations of characters (factor) and calculates the value of each factor for separating the population into groups on the basis of the proportion of the total variance accounted for by each factor.

As in other statistical methods, discriminant analysis depends on certain assumptions, such as multivariate normal distribution of the data and the equality of the group covariance matrices. However, even if these assumptions are not satisfied completely the analysis remains a powerful tool for data analysis. To evaluate the efficiency of an analysis, one can simply look at the graphical representation of the results given as the so-called canonical scores (see below). Furthermore, one can classify the original data according to the results of the group classification analysis. The number of misclassifications is an indication of the degree of overlap between the groups or of some irregularities in the data set.

With canonical functions the information contained in the full character set is compressed into the new scores and a high percentage of the total information is included in a few derived scores. For the graphical representation of the results, we generally use the two most important scores to produce scattergramms if more than two groups were entered for the analysis. An analysis involving two groups produces one-dimensional scores only. In these cases data are presented as probability distribution estimated by a histogram method (van Ryzin 1973).

Results

Skull morphology

The colour of the incisivi (white in *X. inauris* and yellow to orange in *X. princeps*) turned out to be the best discriminant character. The differences in other skull characters of the two species are illustrated in Fig. 1. Additional explanations and comments are given in Tab. 1. Altogether, these characters can be regarded as extremely useful for the identification of skulls (or even certain parts of the skulls) of *X. inauris* and *X. princeps*. The rate of misclassifications is low (0.4–3.0 %); intermediate results occur at a rate of 4.8–22.9 %.

Skull morphometry

Fourteen different measurements were taken from each skull (Fig. 2). Occasionally skulls were damaged and hence only some of their characters could be measured. The results are listed in Tab. 2. An univariate F-test for single characters reveals highly significant differences between the two species in condylobasal length, occipitonasal length, interorbital width, postorbital width, nasalia width and the incisivi diameter (Tab. 3). The most discriminating character is the nasalia width.

The orbital length in 30 skulls of *X. inauris* was shorter than or equal to (0.3 mm–0.0 mm) one third of the occipitonasal length in three cases only and from 0.3 mm to 1.9 mm longer than one third of the occipitonasal length in the remaining 27

cases. In seven *X. princeps*, however, the orbital length was 0.87 mm to 2.3 mm longer than one third of the occipitonasal length.

Discriminant analysis

As the number of skulls (especially of *X. princeps*) examined is rather low, we tested whether males and females had to be analysed separately or could be lumped together. It is apparent from Fig. 3 that there is a large overlap among sexes in both species. Because of

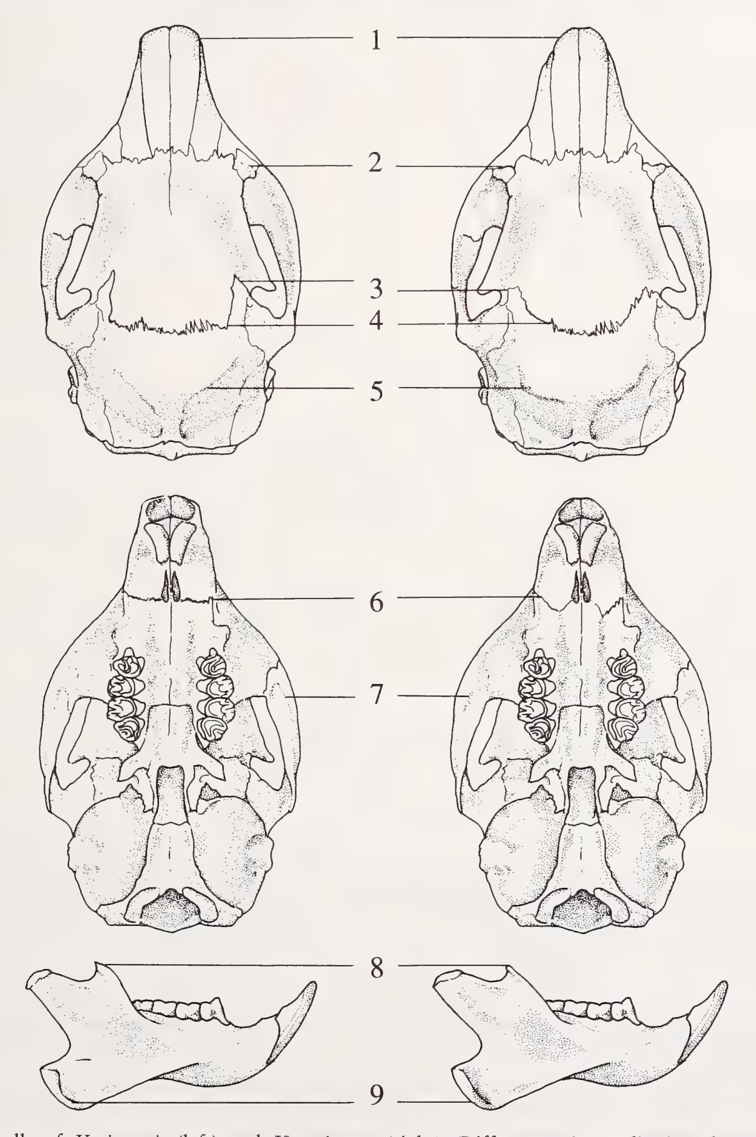


Fig. 1. Skulls of *X. inauris* (left) and *X. princeps* (right). Differences in qualitative characters on cranium and mandible (1-nasalia; 2-lacrimal bone; 3- and 4-fronto-parietal suture; 5-temporal crest; 6-maxillo-praemaxillar suture; 7-base of musculus masseter on zygomatic arch; 8-coronoid process; 9-angular process). See Tab. 1 for further explanations

Table 1. **Differences in qualitative skull characters**
(see also Fig. 1)

Character	*Xerus inauris*	*Xerus princeps*	Comments
Incisivi colour	white; intermediate: yellow tinge	yellow to orange	a good character with no misclassifications
Nasalia – form of the distal end	clearly broader than the proximal end; intermediate: just sligthly widened Fig. 1:1	narrow, not essentially broader than the proximal end Fig. 1:1	a good character; 1,3 % misclassification in *X. i.*; intermediate results in 7.7 % of *X. i.* and 11.4 % of *X. p.*
Shape of lacrimal bone	roundish Fig. 1:2	longish Fig. 1:2	a fairly good character; 0.4 % misclassification in *X. i.* and 2.9 % in *X. p.*; intermediate results in 4.8 % of *X. i.* but in 22.9 % of *X. p.*
Form of fronto-parietal suture – lateral end	pointed Fig. 1:3	rounded Fig. 1:3	a good character; 1.8 % misclassification in *X. i.*; intermediate results in 13.5 % of *X. i.*
Form of fronto-parietal suture – middle part	see Fig. 1:4	see Fig. 1:4	a good character; 0.4 % misclassification in *X. i.*; intermediate results in 4.4 % of *X. i.* and 11.8 % of *X. p.*
Form of temporal crest	see Fig. 1:5	see Fig. 1:5	a good character; 0.4 % misclassification in *X. i.* and 3 % in *X. p.*; intermediate results in 7.7 % of *X. i.* and 12.1 % of *X. p.*
Maxillo-praemaxillar suture	see Fig. 1:6	see Fig. 1:6	a good character
Base of musculus masseter on the zygomatic arch	pointed end Fig. 1:7	roundish end Fig. 1:7	a good character
Shape of coronoid process	see Fig. 1:8	see Fig. 1:8	a good character
Shape of angular process	see Fig. 1:9	see Fig. 1:9	a good character

this and despite the fact that the second axis represents statistically significant ($p < 1$ %) differences between the four groups, the further analysis were performed with all specimens (with complete definitive teeth) irrespective of sex. These individuals of the two species are clearly separated along axis 1 (Fig. 3); within this factor the nasalia width is the character with the highest correlation coefficient and the greatest weight. The variation of scores along axis 2 reflects the differences between different populations and between the different age classes. The main characters within factor 2 are the condylobasal length, occipitonasal length and the orbital width, i.e., measures which reflect growth and differences in growth.

Fig. 4 displays the separation of various *X. inauris* populations and *X. princeps*. The discriminant factor 1 consists mainly of the differences in nasalia width and incisivi diameter (see Tab. 4a). The *X. princeps* skulls are obviously different from all the *X. inauris* skulls. *X. princeps* skulls have the narrowest nasalia width (7.77 mm) and show the largest incisivi diameter (3.9 mm). The *X. inauris* skulls from Namibia are closest to the ones of *X.*

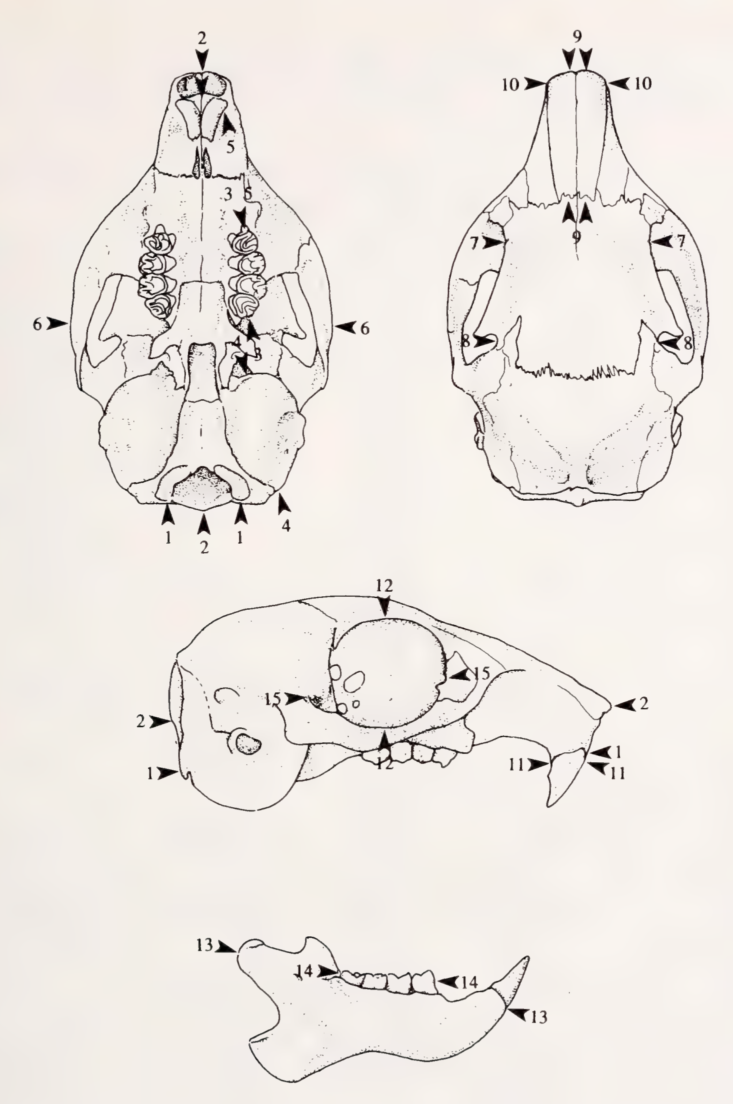


Fig. 2. Measurements taken on cranium and mandible of *Xerus* skulls (1-condylobasal lenth; 2-occipitonasal length; 3-length of upper tooth row; 4-length of bulla; 5-diastema length; 6-zygomatic breadth; 7-interorbital width; 8-postorbital width; 9-nasalia length; 10-nasalia width; 11-incisivi diameter; 12-orbital width; 13-mandible length; 14-length of lower tooth row; 15-orbital length)

princeps (i.e., 8.45 mm and 3.61 mm, respectively). *X. inauris* from Bloemhof (western Transvaal) and the Orange Free State show the greatest distance from *X. princeps* along this axis. Their nasalia width is much larger (9.22 mm and 9.61 mm, respectively) and their incisivi diameter significantly smaller (3.54 mm and 3.49 mm, respectively).

Obvious differences within *X. inauris* skulls occur along the discriminant axis 2 (Fig. 4). The main characters within factor 2 are condylobasal length, occipitonasal length, mandible length, postorbital width, orbital width, interorbital width and zygomatic breadth (see Tab. 4a). *X. inauris* from the Orange Free State show the largest skulls (occipitonasal length 58.28 mm); those from Namibia the smallest ones (occipitonasal

Table 2. **Skull measurements (mm) of *X. inauris* (n = 157) and *X. princeps* (n = 22); specimens with complete permanent dentition**

Mean ($\bar{x}$), standard deviation (± S.D.), 95 % confidence limits (± 95 % C.L.) and range of measurements

	Mean	±S.D.	95 % C.L.	Range
Condylobasal length				
inauris	53.1	1.82	52.8–53.4	47.9–56.9
princeps	54.6	1.38	54.0–55.2	51.4–57.0
Occipitonasal length				
inauris	56.4	1.99	56.1–56.7	51.1–61.3
princeps	58.2	1.53	57.6–58.9	54.6–61.4
Upper tooth row				
inauris	11.4	0.53	11.3–11.5	10.0–12.6
princeps	11.2	0.40	11.0–11.4	10.3–11.9
Zygomatic breadth				
inauris	35.2	1.51	35.0–35.4	31.1–38.6
princeps	35.4	1.02	34.9–35.8	33.4–37.1
Interorbital width				
inauris	17.0	0.86	16.9–17.2	15.1–19.9
princeps	17.9	0.83	17.6–18.3	16.2–19.2
Diastema				
inauris	12.8	0.86	12.7–13.0	11.1–18.8
princeps	13.5	0.59	13.2–13.7	12.4–14.5
Bulla				
inauris	13.2	0.56	13.2–13.4	12.0–14.4
princeps	13.7	1.37	13.1–14.3	12.8–15.1
Postorbital width				
inauris	21.4	0.84	21.3–21.6	19.7–25.2
princeps	22.5	0.39	22.4–22.7	21.8–23.1
Nasalia length				
inauris	19.4	1.01	19.2–19.5	16.2–21.6
princeps	20.1	1.02	19.6–20.5	18.0–22.0
Nasalia width				
inauris	9.0	0.71	8.9– 9.2	7.0–10.5
princeps	7.8	0.28	7.6– 7.9	7.2– 8.4
Incisivi diameter				
inauris	3.6	0.23	3.5– 3.6	3.1– 4.2
princeps	3.9	0.26	3.8– 4.0	3.4– 4.4
Orbital width				
inauris	15.8	0.77	15.7–15.9	14.1–17.5
princeps	16.2	0.58	16.0–16.4	15.2–17.5
Mandible length				
inauris	36.1	1.49	35.9–36.3	32.8–39.4
princeps	36.9	1.29	36.4–37.5	33.5–39.1
Lower tooth row				
inauris	12.2	0.55	12.2–12.3	10.9–13.4
princeps	12.2	0.41	12.0–12.3	11.5–12.9

length 54.91 mm). The overall skull size of *X. princeps* (occipitonasal length 58.25 mm) is very much the same as the measure of *X. inauris* from the Orange Free State. The classification of the original data according to the results of the discriminant analysis reveals an extremely low number of misclassifications (see Tab. 4b). That means one can

Table 3. **Univariate F-test for single characters of the skull (*X. inauris* – n = 157; *X. princeps* – n = 22)** (* significant, ** highly significant)

Variable	F-value	P	
Condylobasal length	14.7124	0.00039	**
Occipitonasal length	17.9930	0.00015	**
Upper tooth row	3.9820	0.04472	*
Zygomatic breadth	0.3447	0.056505	
Interorbital width	21.0348	0.00007	**
Diastema	11.4186	0.00127	*
Bulla	6.6380	0.01049	*
Postorbital width	36.1449	0.00000	**
Nasalia length	8.9001	0.00359	*
Nasalia width	69.2131	0.00000	**
Incisivi diameter	38.9516	0.00000	**
Orbital width	4.8454	0.02723	*
Mandible length	6.2139	0.01303	*
Lower tooth row	0.4726	0.50016	

Table 4a. **Correlations between 14 characters and the discriminant axis 1 and 2, the corresponding weights and F-values of univariate test ($p < 0.05$ for all characters)**

Variable	F-value	Discriminant factor 1		Discriminant factor 2	
		Correlation coefficient	Weight	Correlation coefficient	Weight
Condylobasal length	33.89	−0.088	−0.06601	0.768	−0.08000
Occipitonasal length	36.44	−0.050	0.09359	0.776	0.26067
Upper tooth row	26.08	−0.543	−0.19576	0.425	−0.17675
Zygomatic breadth	39.85	−0.410	−0.04403	0.654	0.03297
Interorbital width	20.38	0.114	0.20683	0.652	0.15982
Diastema	5.44	0.144	0.04152	0.363	−0.13890
Bulla	2.86	0.077	0.01025	0.281	−0.08083
Postorbital width	28.37	0.121	0.01781	0.712	0.23792
Nasalia length	12.94	−0.061	0.02647	0.560	−0.09580
Nasalia width	84.18	−0.880	−0.71432	0.125	−0.35457
Incisivi diameter	16.25	0.550	0.60673	0.145	−0.58604
Orbital width	30.60	−0.272	−0.02983	0.696	0.29341
Mandible length	34.21	−0.234	−0.01852	0.727	0.10528
Lower tooth row	29.22	−0.464	−0.14626	0.554	0.45808

Table 4b. **Classification of the original data according to the above analysis**

Species/Population	Number of Cases	Number of Missclassifications	Correct classifications (%)
Xerus inauris, Bloemhof	34	4	88.2
Xerus inauris, Orange Free State	38	3	92.1
Xerus inauris, Namibia	34	1	97.1
Xerus princeps	22	0	100.0

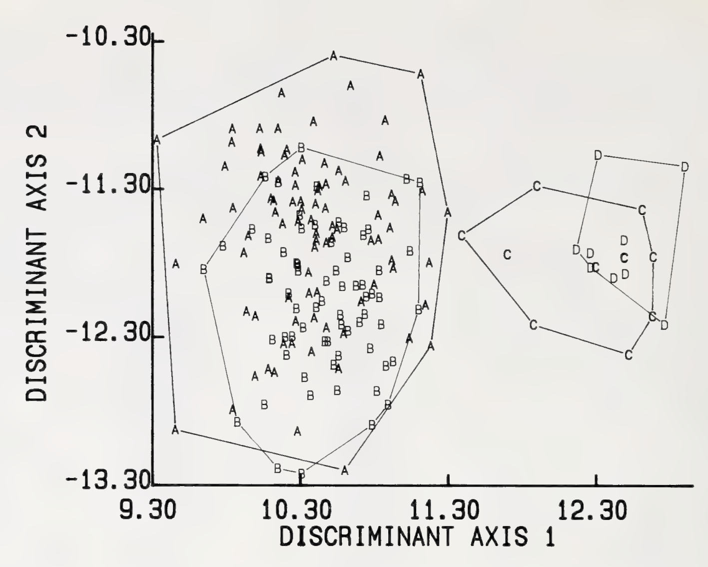


Fig. 3. Separation of *X. inauris* (A – females, n = 88; B – males, n = 69) and *X. princeps* (C – females, n = 10; D – males, n = 9). Analysis is based on 10 characters (multivariate F-test, $p < 0.05$). 98.1 % of the total variance are explained by two discriminant factors

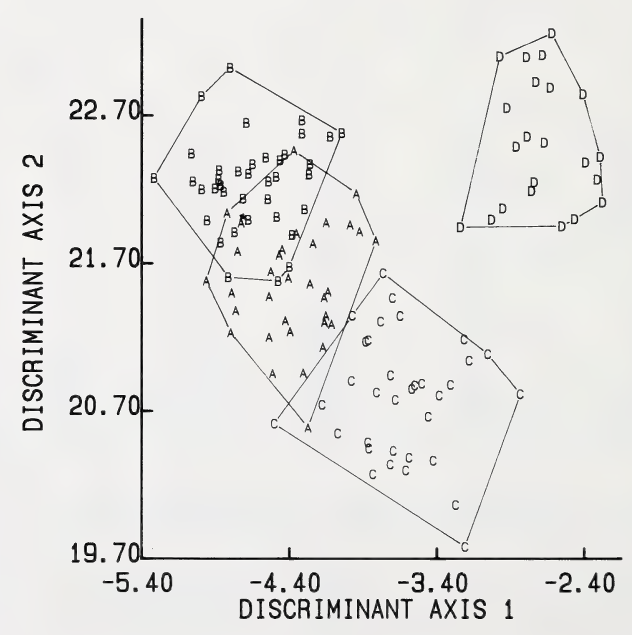


Fig. 4. Separation of various *X. inauris* populations (A – Bloemhof [western Transvaal], n = 34; B – Orange Free State, n = 38; C – Namibia, n = 34) and *X. princeps* (D, n = 22). Analysis is based on 14 characters (univariate F-test, $p < 0.05$); 95.44 % of the total variance are explained by 2 discriminant factors



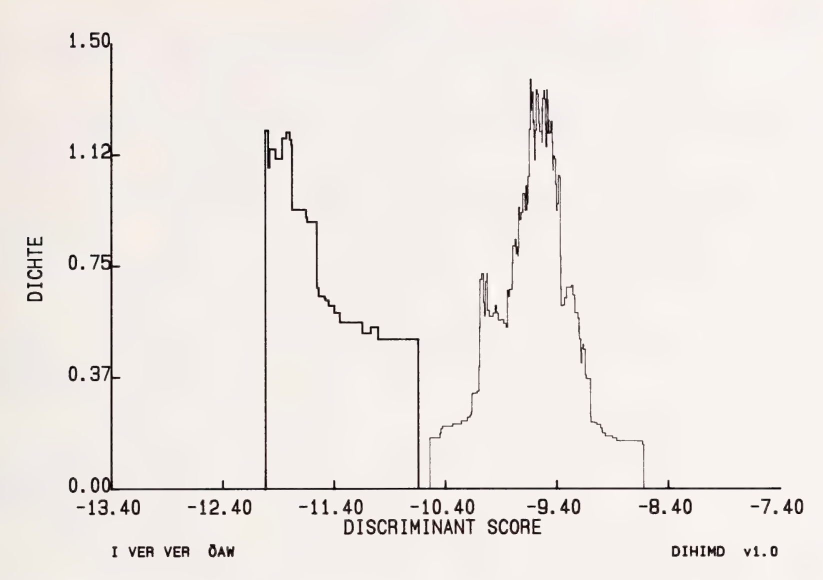


Fig. 5. Separation of *X. inauris* (n = 157; thin line) and *X. princeps* (n = 22, thick line); analysis is based on 12 characters (univariate F-test, $p < 0.05$)

easily discriminate between the skulls of *X. inauris* and *X. princeps*, and the discrimination between the skulls of various *X. inauris* populations is highly successful too.

Finally, the multivariate linear discriminant analysis was applied to all specimens with 12 characters which were significantly different between *X. inauris* and *X. princeps* in the univariate F-test (Tab. 3). As is apparent from Fig. 5, the two species are clearly separated. Within the only discriminant factor nasalia width, incisivi diameter and postorbital width are the characters with the highest correlation coefficients and the greatest weight; the most discriminating measure is the nasalia width (Tab. 5). A reclassification of the data according to this analysis produces not a single misidentification.

Table 5. **Correlations between 12 characters and the canonical discriminant axis and the corresponding weights**

(F-values of the univariate test see Table 3)

Variable	Correlation coefficient	Weight
Condylobasal length	−0.320	0.06115
Occipitonasal length	−0.351	−0.14454
Upper tooth row	0.171	0.19787
Interorbital width	−0.377	−0.18208
Diastema	−0.284	0.00791
Bulla	−0.220	−0.00704
Postorbital width	−0.476	−0.21190
Nasalia length	−0.253	0.00767
Nasalia width	0.613	0.87515
Incisivi diameter	−0.491	−0.23103
Orbital width	−0.188	−0.16309
Mandible length	−0.213	0.11016

Discussion

Although the species identity of *X. inauris* and *X. princeps* has sometimes been questioned in the past recent studies have already supported their recognition as two different species: Robinson et al. (1986) showed a subtle heterochromatic difference between them, Haim et al. (1987) found several significant physiological differences

between them, and recently HERZIG-STRASCHIL and HERZIG (1989) illustrated differences between the two species with regard to habitat selection and social structure.

The above results on the morphology and morphometry of skulls of the two species now again show clear differences between these two ground squirrels which look so very much alike at first sight.

Generally the size of skulls and especially the width of the nasalia and the diameter of the incisivi show some gradient from E (SE) to W (NW) in *X. inauris*: while skulls get smaller and nasalia narrower from the Orange Free State (South Africa) to Namibia, the diameter of the incisivi increases. Skulls of *X. princeps* from Namibia are large (comparable to those of *X. inauris* from the Orange Free State), but also have narrow nasalia and strong incisivi (one could speculate about a correlation of this feature with an arid environment).

Finally, it is amazing that the best discriminating factor apart from the colour of the incisivi, the width of the nasalia, a difference previously recognized by THOMAS (1929) and illustrated by DE GRAAFF (1981), was never used in identification keys, while the relationship of orbital length (also merely called orbit or orbit diameter or eye orbit) to occipitonasal length appeared in most of the keys (e.g., "orbit normally rather less than one third of occipitonasal length in *X. inauris* and normally more than one third of occipitonasal length in *X. princeps*" [ELLERMAN et al. 1953]). The measurement "orbit" is defined by ELLERMAN et al. (1953) and described in more detail as "orbital length" by MOORE (1960), while other keys lack any explanation. The results of some measurements, however, showed that there are differences between the two species but not in the procedures used thus far. This disagreement is probably the result of a still not standardized way of measuring the orbital length.

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Zusammenfassung

Morphometrische Analyse der Schädel von Xerus inauris und Xerus princeps (Rodentia, Sciuridae)

Der Artstatus von *Xerus inauris* und *X. princeps*, die einander äußerlich sehr ähnlich sehen, wurde in der Vergangenheit zeitweise angezweifelt. Um eine Klärung in der Unterscheidbarkeit der beiden Arten herbeizuführen, wurden insgesamt 302 Schädel von *X. inauris* und 49 Schädel von *X. princeps* untersucht. Deutliche qualitative Unterschiede ergaben sich in der Farbe der Incisivi (weiß bei *X. inauris*; gelb bis orange bei *X. princeps*) sowie neun weiteren morphologischen Merkmalen, deren Gebrauch zur Unterscheidung der beiden Arten nur geringe Fehlbestimmungen (0.4–3 %) ergaben.

Schädelmaße von Tieren mit kompletter Bezahnung wurden anschließend einer multivariaten linearen Diskriminanzanalyse unterzogen. Ein univariater F-Test für einzelne Maße zeigt hochsignifikante Unterschiede zwischen den beiden Arten in der Codylobasalllänge, der Occipitonasallänge, dem Interorbitalabstand, Postorbitalbreite, der Breite der Nasalia und dem Durchmesser der Incisivi. Das am stärksten trennende Merkmal ist die Nasaliabreite.

Eine abschließende multivariate lineare Diskriminanzanalyse mit 12 Merkmalen, die im univariaten F-Test signifikant waren, zeigt eine deutliche Differenzierung zwischen diesen beiden Arten, wobei Nasaliabreite, Incisividurchmesser und Postorbitalbreite die stärkste Gewichtung zukommt.

Schädel von *X. inauris* zeigen Unterschiede vom Orange Free State und Western Transvaal bis Namibia: die Schädel werden von Ost nach West kleiner, die Nasalia schmäler und die Incisividurchmesser größer. *X. princeps* in Namibia haben große Schädel, aber ebenfalls schmale Nasalia und große Incisividurchmesser.

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WISSENSCHAFTLICHE KURZMITTEILUNGEN

Diphyodont dentition of first premolar in the Red fox *Vulpes vulpes* (Linné, 1758)

By H. Ansorge

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The diphyodont dentition of mammals shows different modifications in several orders. Within the carnivores, it is especially remarkable for Canidae and Mustelidae that the first (orally situated) premolar appears only once and is not changed like the other premolars.

Thus, the first premolars are not generated in the short tooth row of the fox puppy, but appear not earlier than after 15 to 16 weeks. There is much controversy to which of the two types of dentitions this first premolar belongs. Slaughter et al. (1974) treat the "unreplaced DP1/dp1" as teeth of the milk dentition. Seiferle and Meyer (1942) also interpret the P1 as a late emerging and persisting milk tooth, being equivalent to a permanent tooth in size and form. However, Lüps et al. (1972) emphasize that the P1 is developed only in one generation as a typical permanent tooth and cannot be a persisting milk tooth. Concerning the Red fox, Capt et al. (1980) emphasize the P1 to be the earliest permanent tooth which is not established in milk dentition. Supporting this assumption Hochstrasser (1971) found supernumerary first premolars in the red fox and regarded it as an exceptionally developed and persisting milk tooth. Such persisting milk teeth are also known in primates (Krapp and Lampel 1973). Accepting ontogenetic dental development as embryonic recapitulation of phylogeny (Gängler 1987), it seems likely that a milk-tooth bud developed prior to the emergence of P1 from the secondary dental lamina.

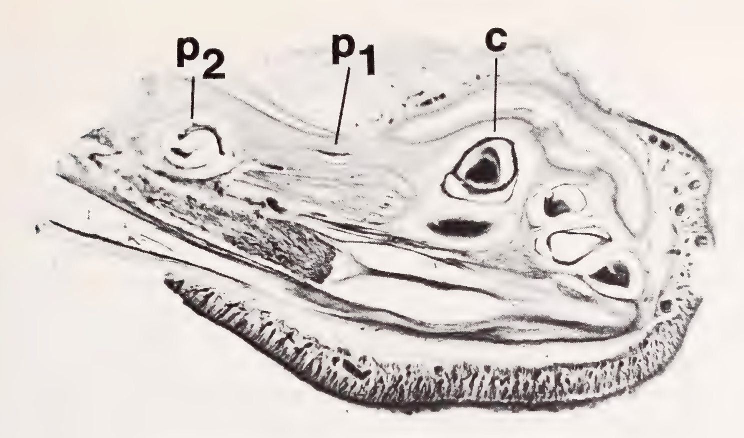
To resolve this problem, the lower jaws of differently aged Red foxes were studied: embryos of 37, 40, 43, 45 and more than 50 days originating from wild vixens as well as 2-week-old puppies from artificial rearings. The age of embryos was estimated according to Layne and McKeon (1956). Series of sagittal sections of paraffin-embedded jaws enabled the identification of dental cups.

The 37-day-old embryo possesses already well-differentiated dental cups of canines and incisors. Alterations in jaw structure suggest future emergence of two premolars.

The lower jaw of the 40-day-old embryo shows all dental cups of the complete deciduous dentition. Almost equidistant from p_2 and canine cups, a small lenticular tissue structure is situated in a bone loosening at the same horizontal level. This structure must be regarded as p_1 bud as investigation of older embryos showed. This dental bud appears unchanged in the serial sections of the 43-day-old embryo, whereas the other dental cups experienced further size growth and differentiation (Fig.).

The dental cup of p_1 does not change during the further embryogenesis. In the lower jaw of most developed fetuses it is clearly recognized and situated dorsal to the proximal end of the canine, directed skewly anteriorly. It has only slightly increased (0.37 mm diameter) but shows no further differentiation. Therefore, this indicates a rudimentary tooth bud. At the same time, the canine, for example, already shows a typical tooth appearance.

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Sagittal section of the red fox lower jaw (43-day-old embryo)

In sections of the 2-week-old fox puppy the dental bud of permanent P_1 is clearly perceptible, beside the M_1 germ. It is situated far buccal in the jaw. The deciduous p_1 tooth bud of the older embryos placed lingually between canine and second premolar has dissolved. It cannot be identical with this permanent tooth bud.

Therefore, the first premolar appears in the deciduous dentition of the red fox at about the 40th embryonic day. This tooth shows no further differentiation and remains in the jaw as a rudimentary tooth bud. It dissolves in the first two weeks after birth. Thus, the red fox shows a complete diphyodont dentition by secondary suppression of the first premolar.

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The scientific name of the Bontebok

By L. C. Rookmaaker

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"I have begun to run over all the Cabinets, and to collect whatever seems remarkable to me with regard to the Quadrupeds", the young Peter Simon Pallas (1741–1811) wrote from Holland to Thomas Pennant on 18 January, 1766 (Urness 1967). Pallas found a rich treasure of interesting animals in the large number of private cabinets in Holland and in the museum of the Prince of Orange. The results of his investigations were laid down in the Miscellanea Zoologica of 1766. In the first chapter of that book he described 17 species of antelopes, eight of which today still bear the names he proposed at that time following the (then) new system of classification introduced by Linnaeus. He must have received a number of comments about his work, because Pallas immediately began to revise the text: "Er sagte es scheine ihm, daß jenes Werk diese Verbesserung bedürfe, daß er sich selbst nicht genug gethan, und daß ihm vornemlich die Kupferstiche misfielen. Diesen Entschluss machte er im Mai 1767, und also kurz vor seiner Abreise nach Petersburg bekannt" (C. G. Baldinger in Pallas 1767). The revised book, the Spicilegia Zoologica, appeared in installments: the issue on antelopes in 1767. Pallas made quite a number of changes in the text and in the classification: he renamed three species, he deleted two, and he separated one species into two.

In the Miscellanea, Pallas (1766) described the *Antilope dorcas* after "integras ... pelles" (undamaged skins). His statements about the morphology of the horns, the colour of the body and the size of the animal show beyond doubt that he must have examined skins of the antelope now called bontebok. He called it *Antilope dorcas*, because he assumed that it was identical with the 'dorcas' of the ancients, and by implication with the *Capra dorcas* of Linnaeus (1758). In the revised Spicilegia, Pallas seems to have realised that he had combined two species in his *A. dorcas* or rather that the 'dorcas' of the ancients could not have been the animal from which he had examined the skins. He retained *A. dorcas* for the animal found in the old texts (but he did not describe it further), and he now gave a new, but essentially similar description of the bontebok skins under the new name *Antilope pygargus* (Pallas 1767). Incidentally, it seems that Pallas was rather casual in his nomenclature, which may need some further study; he mentioned in his note on *Antilope dorcas* that the dorcas [= *Capra dorcas*] of Linnaeus to him appeared to be the same as the antelope which he had called *Antilope bubalis* in 1767 (or *A. buselaphus* in 1766).

The change by Pallas from *A. dorcas* in 1766 to *A. pygargus* in 1767 has been the cause of much nomenclatorial confusion. During the 19th century, the bontebok was generally referred to as *Antilope pygarga*, with some changes in the genus name. Sclater and Thomas (1894–1900) gave a very succinct and correct exposition of the understanding at that time: "In his first essay on the genus *Antilope*, published in 1766, Pallas described it as *Antilope dorcas*, having confounded it with the *dorcas* of Aelian. But in his second essay upon the same group, issued in the following year, he selected for it the very appropriate name *pygarga*, by which it has been generally known ever since."

This problem was reviewed again by Harper (1940). He argued that *A. pygargus* was correct in the 19th century, because *A. dorcas* Pallas, 1766 then was preoccupied by *Antilope* [= *Capra*] *dorcas* Linnaeus, 1758. However, when the two species were referred to different genera, *A. dorcas* Linnaeus to *Gazella*, and *A. pygargus* Pallas to *Damaliscus*,

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"the *dorcas* of PALLAS becomes available again ... and the combination to be used henceforth is *Damaliscus dorcas* (Pallas). *A. pygargus* becomes a synonym." This has been generally followed since then and the bontebok has been referred to as *Damaliscus dorcas* (PALLAS, 1766).

Based on Article 59(b) of the 1985 Code of Zoological Nomenclature, I advanced a different argument (ROOKMAAKER 1989). These matters of homonymy are never easy to settle, especially when it concerns 18th century authors like PALLAS who did not yet have a nomenclatorial code. One could argue, however, that PALLAS in his Spicilegia Zoologica of 1767 intended to differentiate two species, the dorcas gazelle and the bontebok. He used the existing name *A. dorcas* for the first of these. He had earlier referred to the bontebok with this same name, but in 1767 he could no longer do so as the name had already been used for another species, i.e. *A. dorcas* for the bontebok was a secondary homonym. PALLAS then renamed the animal, without explicit explanation, to be called *Antilope pygargus*. According to the present Code of Nomenclature, a junior secondary homonym once replaced (before 1961) is permanently invalid. For that reason, *A. dorcas* cannot now be used for the bontebok and that species should be called *Damaliscus pygargus* (PALLAS, 1767).

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BUCHBESPRECHUNG

Klein, R. G.: **The Human Career.** Human Biological and Cultural Origins. Chicago, London: University of Chicago Press 1989. 524 pp., num. illustrations US$ 45.95. ISBN 0-226-43962-3

Das Buch will weder eine Einführung noch ein Handbuch sein. Es entspricht am ehesten einem Kursus für „graduate students" und behandelt, wie der Untertitel zeigt, Paläoanthropologie und Urgeschichte. Dadurch unterscheidet sich das Buch von zahlreichen ähnlichen Werken. Der Autor, Professor für Anthropologie an der Universität Chicago, ist vor allem durch seine Arbeiten über die Steinzeit Eurasiens und Afrikas und durch das gemeinsam mit P. S. Martin herausgegebene Werk „Quaternary extinctions: a prehistoric revolution" (1984) bekannt geworden.

Zum Inhalt: Nach dem Vorwort wird der erdgeschichtliche Rahmen (samt Altersdatierung und Paläoklimatologie) ausreichend und die Geschichte der Primaten von der Oberkreide bis zum Jungmiozän ausführlich behandelt. Der Hauptteil (Kap. 3–8, S. 100–410) ist den fossilen und rezenten Hominiden (der Begriff Hominidae wird [richtigerweise] nur für bipede Primaten, also Menschen, und nicht auch für Menschenaffen verwendet) gewidmet. Zwei Anhänge (Klassifikation und Nomenklatur; Technik und Typologie von Stein-Artefakten) ergänzen den Text. Ein ausführliches Literaturverzeichnis (auch mit deutschsprachigen Zitaten) (S. 428–492) und ein dreiteiliger Index erhöhen Wert und Benutzbarkeit des Buches.

Die Primaten gliedert der Verfasser (nach Gingerich [1984] in Praesimii (Tupaiiformes und Plesiadapiformes einschl. Microsyopidae [!]), Prosimii und Anthropoidea, also Halbaffen und Affen nicht in Strepsirhini und Haplorhini (Hinweis nur im Text vorhanden). Auf Probleme, die sich aus widersprüchlichen morphologischen und biomolekularen Refunden für die Evolution ergeben, wird hingewiesen. Nach Fig. 2.22 war das „knuckle-walking" auch bei den menschlichen Vorfahren ausgebildet, sofern man nicht eine unabhängige Entwicklung bei Gorilla und Pan annimmt. Die vermutlichen Gründe für die Bipedie der Hominiden werden eingehend diskutiert. In Zusammenhang mit der Diskussion um die Schmelzdicke bei Pongidenmolaren wird eine „readaptation" an stärkere (Ur-)Waldbedingungen bei den heutigen afrikanischen Menschenaffen angenommen.

Die Australopithecinen werden ausführlich besprochen. *A. afarensis* wird als einheitliche Art und gemeinsame Stammform der übrigen *A.*-Arten angesehen. *A. „aethiopicus"*, *A. robustus* und *A. boisei* werden als eigene Arten der *„robustus*-Gruppe" *(Paranthropus)* klassifiziert. Die sog. „osteodontokeratische Kultur" der Australopithecinen wird nicht als Gerätekultur, sondern als wahrscheinliche Lebensspuren von Hyänen angesehen. (Man vermißt die grundlegende Arbeit von Zapfe [1939] ebenso wie jene vom Rez. [1961].) Bei *Homo habilis* wird auf die Problematik dieser Art in morphologischer, taxonomischer und phylogenetischer Hinsicht hingewiesen. *Homo erectus* (Problem: biologische Art oder nur ein Stadium?) ist nach Verf. nur aus Afrika und Asien nachgewiesen. Während aus afrikanischen *H. „erectus"*-Populationen der „moderne" Mensch *(Homo sapiens)* hervorgegangen ist, werden die (eigentlichen) *H. erectus*-Formen aus Ostasien als evolutiver Seitenzweig angesehen. Die europäischen alt- und mitteleiszeitlichen Hominidenfunde (z. B. Mauer, Petralona, Vertesszöllös, Bilzingsleben, Swanscombe, Steinheim) werden sämtlich dem frühen *H. sapiens*-Formenkreis („early *Homo sapiens*") zugeschrieben. Der Neandertaler *(Homo sapiens neanderthalensis)* ist in typischer Form auf Europa und den Nahen Osten beschränkt. Er verfügte wahrscheinlich nicht über eine Sprache wie der moderne Mensch, war jedoch der erste Mensch, der verstorbene Angehörige bestattete. Der anatomisch (gehirnmäßig) moderne Mensch *(Homo sapiens sapiens)* ist vermutlich in Afrika entstanden. Er erscheint vor etwa 35 000 Jahren in Europa (z. B. Cromagnon, Combe-Capelle).

In den Hauptkapiteln werden nicht nur Morphologie und Vorkommen, sondern auch Lebensraum, Lebens- und Ernährungsweise, Verhalten, Krankheiten, Sterblichkeit, vermutliche Sozialstruktur und Kunst berücksichtigt. Besonders ausführlich wird auf die Artefakte und auf den Feuergebrauch eingegangen und auf die verschieden rasche Geschwindigkeit der kulturellen Evolution, die sich in der Werkzeugherstellung widerspiegelt, bei *H. erectus* und *H. sapiens* hingewiesen.

Die neuen Lokalnamen von Fundstellen sind neben den gebräuchlichen alten durchweg berücksichtigt (z. B. Zhoukoudian-Choukoutien, Tighennif-Ternifine, Perning-Modjokerto).

Leider ist die Primärliteratur, die für die jeweilige Entdeckungsgeschichte wichtig wäre, nicht immer zitiert (z. B. Berckhemer, Fuhlrott, Gorjanovic-Kramberger, Schoetensack, Thoma).

Alles in allem ein Buch, das – trotz der obigen Kritik – allen wärmstens empfohlen werden kann, die sich näher für die biologische und kulturelle Evolution des Menschen interessieren.

E. Thenius, Wien

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Zusätzlich erscheint einmal im Jahr ein Heft mit den Abstracts der Vorträge, die auf der jeweiligen Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde gehalten werden. Sie werden als Supplement dem betreffenden Jahrgang der Zeitschrift zugeordnet. Verantwortlich für ihren Inhalt sind ausschließlich die Autoren der Abstracts.

Manuskripte: Manuskriptsendungen sind zu richten an die Schriftleitung, z. Hd. Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Biologie-Zentrum, Neue Universität, Olshausenstr. 40–60, W-2300 Kiel, Bundesrepublik Deutschland. Für die Publikation vorgesehene Manuskripte sollen gemäß den „Redaktionellen Richtlinien" abgefaßt werden. In ihnen finden sich weitere Hinweise zur Annahme von Manuskripten, Bedingungen für die Veröffentlichung und die Drucklegung, ferner Richtlinien für die Abfassung eines Abstracts und eine Korrekturzeichentabelle. Die Richtlinien sind auf Anfrage bei der Schriftleitung und dem Verlag erhältlich.

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Notes on reproduction of captive *Bassariscus sumichrasti* (Procyonidae)

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Abstract

Studied the reproductive behavior, including precopulatory and copulatory behavior, as well as estrous cycles in captive *Bassariscus sumichrasti.* Average duration of estrus is 44.4 days. Fertilization is possible only during a single day. ♂♂ mount estrous ♀♀ 5 to 30 days before the ♀♀ are able to conceive. These mountings are resisted by the ♀♀, and most if not all, do not lead to intromission. One to 2 successful copulations terminate the pair's sexual activities. It is hypothesized that *B. sumichrasti* ♀♀ may have induced ovulation, released by prolonged periods of frequent sexual stimulation by the ♂. The gestation period was determined to be 64 to 66½ days. Births of singletons are the rule.

Introduction

The Central American or tropical cacomixtle, *Bassariscus sumichrasti,* has been rarely kept in zoos or private collections. Breeding success in captivity has been limited. This paper reports on the reproductive behavior of captive *Bassariscus sumichrasti,* compared with that of captive *Bassariscus astutus.*

B. sumichrasti is an arboreal, nocturnal, omnivorous carnivore. It is recognized as a solitary animal (Alvarez del Toro 1977; Poglayen-Neuwall, pers. observ.), but a feeding aggregation of 9 individuals in a fruiting tree without conflicts among the animals has been observed (R. Morales, pers. comm.).

Material and methods

Six ♂ and 3 ♀ Central American captive cacomixtles were observed over periods of up to 19 years in order to compile an ethogram for the species. Animals were kept singly, in pairs of opposite and same gender, in enclosures of 2×2×2, 6×8×2, and 2×3×2 m. Three of the cages were located outdoors, 4 indoors. Outdoor cages had natural soil substrate, all others cement floors. Each cage was structured with climbing branches, and at least 2 wooden, elevated sleeping boxes with 2 clear plastic viewing panels. Because of the extreme heat (up to 45 °C) and aridity of southern Arizona, outdoor enclosures were well shaded and provided with either evaporative coolers or overhead water misters. For protection from inclement winter weather (rarely more than 3 degrees below freezing at night) outdoor enclosures were covered on all sides with plastic sheeting, with closeable openings on one side for observation. Heat lamps were used when necessary.

Animals were fed in the evening a mixture of selected fruits, dry dogchow softened with water, a fresh-killed chick, occasionally a small rodent, quail eggs and insects (beetles, grasshoppers, crickets, moths). Dried skim milk, a calcium-phosphate powder and multivitamins were added to the rations. Fresh water was always available.

Photographs were taken with Nikon F2 and F3 cameras and strobe light if necessary, and observations were taken down on note pads or tape recorders. Photoperiods were not artificially manipulated.

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Results and discussion

A captive pair of Honduran *Bassariscus sumichrasti variabilis* ("Nuevo" and "Honda") was observed by the author, copulating on 9 February 1974, 1600 h. During the following 2 days the ♀ evaded the ♂, and on the third day postcopulam the ♂ had lost all interest in the ♀. Total duration of this estrus was 34 days ("estrus" in this paper comprises proestrus, estrus and metestrus; no effort has been made to differentiate the various stages). The copulation was preceded by 14 days of numerous brief mountings of the recalcitrant ♀. These mountings occurred throughout the night, each lasting only a few seconds, and none leading to intromission (Fig. 1). On the average, 24 mountings/h were registered. On 9 February the animals were already active at 1530 h when 11 attempted copulations were observed within 3.5 min. Typically, ♂ mounts and attempts intromission 5 to 30 days before the ♀ becomes receptive. Until maximum tumescence of the vulva is attained the ♀ thwarts all mating attempts of the ♂ by turning, rolling onto her back, geckering, squealing, and finally escaping the ♂'s clasp. As an example may serve a captive ♂ *B. s. variabilis* and a ♀ *B. s. sumichrasti*: the ♂ was introduced to the ♀ a week before she had reached the peak of estrus. On the 3rd day the ♂ started to pursue the ♀. Within a 40-min observation period the ♂ made 47 unsuccessful attempts to copulate. Until the resistance of the ♀ was overcome 4 days later (the 30th day of estrus), 280 mounting attempts were noted. The true number was certainly considerably higher since counts were not carried out during the entire activity period of the animals. The ♀'s vulva had returned to the anestrous state by the 42nd day.



Fig. 1. Copulatory position. Note ♂ grasping skin of nape with teeth to hold/position ♀

A copulatory bout per se takes up to 6 min or longer, and in principle does not differ from that in *B. astutus*, as described by Bailey (1974) and Poglayen-Neuwall (1987), except that there is no evidence of continual vocalizing of the ♀, comparable to the "matting chitter" of the ♀ *B. astutus*. It may be that *B. sumichrasti* is an induced ovulator, the ♀ requiring long and intense sexual stimulation. Successful copulations are few, I observed only one in one ♀, and 2 in another; they are confined to 24 h of the ♀'s reproductive cycle. Another procyonid, *Procyon lotor*, of the temperate and subtropical life zones, copulates 3 to 4 days consecutively (Poglayen-Neuwall, pers. observ.). It is believed to be the only induced ovulator in the family (Llewellyn and Enders 1954). However, Sanderson (1983) asserts that *P. lotor* is a spontaneous ovulator.

Sexual activity during daylight hours is not an artefact of captivity of this otherwise strictly nocturnal species, since a copulating pair of *B. sumichrasti* was observed in a tree about 1600 h in late April in SW Chiapas (P. ALEGRIA, pers. comm.).

Mounting in play context was seen repeatedly in 2 unrelated ♂♂, about 15 months old, mostly conducted by the dominant individual. I also observed pseudo-copulatory mountings, especially in the ♂ "Nuevo", whenever a ♀ was introduced or reintroduced, regardless of whether she was in heat or not. Approach and mountings were always accompanied by characteristic reassuring chirps of the ♂. Naso-nasal contact and mutual sniffing of various body parts are common in this situation. In the case of an anestrous ♀ these interactions may last several min, mounting attempts are perfunctory and repelled or evaded by the ♀.

The reproductive strategy of the ♂ *B. sumichrasti*, attempting copulations many days prior to the receptivity of the ♀, markedly differs from the copulatory pattern of *B. astutus*, whose attempts at copulation are restricted to a 24-h-period, and the ♂ is almost always successful in achieving penetration early (POGLAYEN-NEUWALL 1987).



Fig. 2. ♂ sniffing ♀ ano-genitally prior to mounting

In *B. sumichrasti* the ♂ tests the estrous condition of the ♀ by licking her urine off the substrate, and sniffing or licking over her feces. After testing, the ♂ sometimes raises his head for up to 3 sec, but I have not observed the grimace typical of flehmen. Brief sniffing of their own feces outside the sexual context is common in both sexes immediately after elimination. Initially, the ♂ makes naso-genital contact with the ♀ (Fig. 2), also sniffs along her tail, uttering incessant appeasing chirping, to which the ♀ only rarely responds with the same vocalization. The ♂ may lick over the ♀'s vulva, neck and shoulder region, with the ♀ eventually reciprocating with brief grooming of the ♂'s head, and sniffing at his ano-genital area. The posterior aspect of the semi-pendulous, large scrotum, being bald, pinkish and very conspicuous in *B. sumichrasti*, has undoubtedly a signalling function. During her estrus the ♀ sniffs at the scrotum more often than at the penal area. By comparison the scrotum of *B. astutus* is considerably smaller relative to the animal's size, and the posterior section almost totally haired and thus not conspicuous. The ♀ seems to be less interested in the scrotum of the ♂ in this species. Frequently, between mating bouts, ♂♂ sit upright on their haunches, less often crouched across a tree limb, licking their genital area with or without unsheathed penis, even when no prior vaginal contact

had occurred. The ♀♀ likewise groom their vaginal area after most mountings, whether successful or not, sitting on the small of their back, hind legs straddeled.

It is noteworthy, that the Honduran pair "Nuevo" and "Honda" bred only once successfully, although 5 estrous periods with extensive sexual activity occurred, including one estrus 14 days postpartum, i.e. 10 days after the death of the infant. Twenty subsequent estrous cycles (1973, 1979, 1980, 1982, 1984 twice, and thrice during 1981, 1983, 1985), when associated with another Honduran ♂, did not result in pregnancy despite countless mountings by this new ♂. No observations were made from September 1986 till September 1987, thus only one estrus was recorded for the year 1986. In 1988 "Honda", then approximately 18 years old, had her last estrus. In *B. astutus* the last estrus was observed at the age of 10 years (D. Giuliani, pers. comm.). This may be explained by the markedly shorter life expectancy (in captivity) of *B. astutus* (16 years 6 months) than that of *B. sumichrasti* (over 24 years) (Poglayen-Neuwall 1989).

If a raccoon (*Procyon lotor*) fails to mate during her first estrus of the year, she may go through a second estrus later in the same year (Sanderson and Nalbandov 1973) but not a third cycle. Among the sexually mature, nulliparous and multiparous *B. astutus* in the collection of this writer, not a single one showed evidence of a second estrus within the same calendar year; all were late winter or spring cycles. A *B. astutus* at the New Orleans (Louisiana) and one at the Norfolk (Virginia) zoos, that once gave birth in September, also had only one estrus in the year; supposedly none of these were postpartum cycles (R. Hoyt, C. Sweet, pers. comm.).

During the observed cycles of 1979–1988 the ♀ "Honda" and her second mate demonstrated ambivalent sexual behavior. The ♀ often solicited the ♂, approaching with chirping vocalizations and mounting him, sometimes also carrying out a brief bout of pelvic thrusts (Fig. 3). The ♂ always twisted free, uttering loud gecker vocalizations, characteristic of the non-receptive ♀. Both animals thus acted out reversed roles.

Data for 3 ♀♀ show that estrus occurred in every month of the year, most in March, April, May and June. Duration of estrus, based on vulval morphology and copulatory behavior, was 44.4 days (range = 22–69 days; n = 29). Since more than one estrus per year



Fig. 3. Estrous ♀ mounting/soliciting ♂

has so far been observed in these 3 ♀♀ only, not counting one postpartum cycle, it would be too early to infer that this species is polyestrous.

In comparison with *B. astutus* I found that *B. sumichrasti* do not have testicular regression (checked by periodic palpation of 4 mature ♂♂) retain sexual libido, and, considering also the October birth at a Guatemala zoo, may thus have spermatogenesis throughout the year. Histological examinations of testes/epididymides at different times of the year are planned.

A ♀ *B. sumichrasti sumichrasti*, "Pinta", was taken with her mate from the same tree hole near Sontecomapán, southern Veracruz, on 19 April 1989. The ♀ showed extreme vulval swelling, and copulations took place soon afterward in a small cage. They did not produce offspring. I assume, if conception occurred, that stress of capture and transport caused resorption of the embryo in an early state. An estrus of this ♀ from 8 March to 13 April 1990, and a second one from 7 July to 5 August was likewise non-preductive. Another ♀, "Vera", acquired in March 1989 showed estrus from 2 April to 13 May 1990, at which time she conceived. The 29-day-old infant of this ♀ had to be removed for hand-rearing on 30 July. On 9 August "Vera" entered a new cycle (duration 22 days). Her previous mate was re-introduced and numerous attempts at copulation were observed during several days. Reproductive behavior began in the afternoon, the earliest copulation attempt at 1350 h, and lasted throughout the night with only brief rest periods, until approximately 0400 h. This estrus cannot be called "postpartum" nor "postlactation" estrus, as it does not fit into the time frame of either. It did not result in conception.

After a gestation period of 66 days 13 hours a young was born to "Honda" (sired by "Nuevo") on 16 April 1974 at 0600 h (Fig. 4). The 1990 litter of "Vera" (sired by a Chiapan ♂) likewise consisted of a single ♂ offspring. This young was born on 3 July 1990, at 1345 h, after a gestation of 64 days. These gestation periods contrast with those of 51 days 8 h to 54 days reported for *B. astutus* (Poglayen-Neuwall and Poglayen-Neuwall 1980).

Bassariscus sumichrasti births have been recorded at the regional zoo in Tuxtla Gutiérrez, Chiapas (April 1959) of an 11-year-old ♀ (M. Alvarez del Toro, pers. comm.), and at the Auto-Safari Chapin, Guatemala, 15 October 1988, 5 May 1989, and 8 May 1990 (F. Berger, pers. comm.). In each case singletons were born of which only the last



Fig. 4. 3-day-old ♂; weight: 40.5 g

mentioned, a ♀, survived. The occurrence of litters of single young in *B. astutus* is uncommon. ARANDA and MARCH (1987), GAMERO-IDIAQUEZ (1978), GAUMER (1917), HALL (1981), and JANSON (1981) quote the number of young to be 2 to 4; ALVAREZ DEL TORO (1977) mentions 1 to 2, 3 being the exception. A ♀ collected (field number 3502) by G. G. MUSSER on 17 March 1965 near Las Tuxtlas, Veracruz, and deposited at the Zoology Museum, Univ. Michigan, Ann Arbor, carried 4 embryos of 70–75 mm head-rump length, which I assume would have been born in early April. Since ♀ *B. sumichrasti*, unlike ♀ *B. astutus* with 4 teats, possess only 2 inguinal teats, and the size of the fetuses reported in the field notes of MUSSER would be too large for possible resorption, it cannot be excluded that these fetuses were taken from another species and erroneously attributed to the ♀ quoted.

Months of birth are thought to be March (GAUMER 1917) and April–July (ALVAREZ DEL TORO 1977). HALL (1981) assumes breeding to take place in January. Although the sample is still small, clearly there is a concentration of reproduction (estrous cycles, matings, and births) from February to July inclusively.

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Zusammenfassung

Bemerkungen zur Fortpflanzung von Bassariscus sumichrasti (Procyonidae) in Gefangenschaft

Das Fortpflanzungsverhalten von *Bassariscus sumichrasti*, einschließlich Präkopulations- und Kopulationsverhalten, sowie Östruszyklen wurden untersucht. Die durchschnittliche Länge des Östrus beträgt 44,4 Tage. Befruchtung ist nur an einem Tag möglich. ♂♂ versuchen, mit ♀♀ während deren Hitze bereits 5 bis 30 Tage, bevor diese empfangen können, zu kopulieren. Die ♀♀ wehren sich in diesem Stadium erfolgreich gegen die aggressiven ♂♂, so daß es kaum zur Intromissio kommt. Erfolgreiche Kopulationen während des Gipfels des Östrus beenden schließlich die sexuelle Tätigkeit des Paares. Es wird angenommen, daß *B. sumichrasti* einen induzierten Eisprung hat, der durch eine längere Periode häufigen Aufreitens des ♂ ausgelöst wird.

Die Tragzeit für diese Art wurde mit 64 bis 66½ Tagen festgelegt. Einzelgeburten sind die Regel.

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Zur Größe des Aktionsraumes von *Microtus arvalis* (Pallas, 1779)

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Eingang des Ms. 4. 3. 1991
Annahme des Ms. 8. 4. 1991

Abstract

Home-range size of Microtus arvalis (Pallas, 1779)

Investigated the home-range size of *Microtus arvalis* on slopes of road-sides in agricultural land east of Vienna, and on the flood-water-dam of the Danube in the adjoining river-side-forests. Sites were chosen for laying out plastic tubes, baited with a mixture of shredded coloured wool fibres and soft cheese, at intervals of 447 m. In the next 3 days 150 traps were set out between the plastic tubes, at intervals of 3 m. 4 of these lines were layed out simultaneously on the north, resp. south sides of a road, resp. the dam. These experiments were repeated six times, at monthly intervals in the summer of 1987, always at different places. In that year the density of *Microtus arvalis* was slightly above average.

The presence of coloured wool fibres in stomachs and intestines of the caught voles was controlled. Compared with the results from literature, based on investigations of individually marked voles in small experimental plots, the home ranges were at least ten times greater in this study. These results correspond in general with those of Andrzejewski and Babinska-Werka (1986) regarding bank voles in Polish woodlands. Our voles regularly crossed asphalt road surfaces.

Further experiments with longer trap lines are necessary. In general it is evident, that trap lines have a wider range of attraction than had been thought up to now.

Einleitung

Die heute allgemein akzeptierten Vorstellungen über die Aktionsräume der Feldmaus *Microtus arvalis* (Pallas, 1779) und kleiner Nagetiere überhaupt fußen auf Untersuchungen, die sich des Wiederfanges individuell markierter Tiere auf Probeflächen bedienen. So wird z. B. von Niethammer und Krapp (1982) eine Größe der Aktionsräume (ad. ♂♂ = 1200–1500 m^2; ad. ♀♀ = 300–400 m^2; Jungtiere = 200–300 m^2), wie sie Reichstein (1960) angibt, zitiert. Erlinge et al. (1990) kommen für Erdmäuse (*Microtus agrestis* L., 1761) in Schweden in Abhängigkeit von Fortpflanzungsaktivität und Dichte auf Aktionsräume zwischen 500 und 1500 m^2. Beobachtungen über eine höhere Mobilität (z. B. Spitzenberger 1966) werden meist mit der Existenz „migrierender" Individuen erklärt, während die „seßhaften" die zitierten kleinen Aktionsräume hätten. Neuerdings haben Andrzejewski und Babinska-Werka (1986) für Rötelmäuse (*Clethrionomys glareolus* Schreber, 1780) gezeigt, daß die Aktionsraumgröße mit Hilfe der Markierungsfang-Methode auf den üblichen kleinen Probeflächen nicht erfaßt werden kann, da die Tiere bald nach ihrem Erscheinen auf der Erdoberfläche in einer der ihnen vom Anködern her bekannten Falle gefangen werden und damit die Größe ihres Aktionsraumes gar nicht „zeigen" können. Die zitierte Untersuchung ergab, daß Rötelmäuse, auch fortpflanzungsaktive ♀♀, regelmäßig Entfernungen bis etwa 300 m zurücklegen. Größere Distanzen wären mit der verwendeten Methode nicht nachzuweisen gewesen. Die Autoren haben in einem 200 ha großen Föhrenwald Nordostpolens eine 1,2 km lange Gerade abgesteckt und je 300 m von den Enden entfernt, 3 Tage vor Fangbeginn und während der 5 Tage des Fanges, Hafer als Köder angeboten. Die in 60 auf der Geraden gleichmäßig verteilten Schlagfallen erbeuteten Tiere konnten auf das Vorhandensein von Hafer im Magen untersucht werden. Angeregt durch diese Arbeit, wurden vorliegende Untersuchungen östlich von Wien an Feldmäusen durchgeführt.

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Material und Methode

Da für die Studie Experimente in monatlichem Abstand durchgeführt werden sollten, kamen Äcker nicht in Frage. Große Wiesen existieren in der flachen Ebene des Marchfeldes (≈ 150 m NN) nicht mehr, so daß für die Untersuchungen nur die „linearen" Böschungen von Straßen zur Verfügung standen. Von April bis Oktober 1987 wurden 6 Versuche, jeweils gleichzeitig an Böschungen von Straßen und des Hochwasserschutzdammes, unternommen. Nur Abschnitte mit nord- bzw. südexponierten und damit in Klima und Vegetation markant verschiedenen Böschungen wurden verwendet. Deshalb wurde immer je eine Fallenlinie auf einer Süd- und auf einer Nordböschung ausgelegt (Abb. 1). Es wurde darauf geachtet, daß die beiden Fallenlinien mindestens 800 m voneinander entfernt waren, meist waren es mehrere Kilometer. Jede Stelle wurde nur einmal verwendet. Die Straßenböschungen liegen im ausgeräumten offenen Ackerland (97 % der Fläche sind Felder). Sie wurden zwei- bis dreimal jährlich von der Straßenverwaltung gemäht. Vom Damm, der im Auwaldgebiet liegt, wurden nur solche Stellen gewählt, die durch Wald gut von den Feldern des Ackerlandes abgeschirmt sind. Stellenweise grenzen extensiv genutzte Wiesen an. Eine Mahd erfolgte hier ein- bis zweimal. Manche Abschnitte waren durch südlich angrenzenden Wald beschattet, so daß hier, wie auch an den Nordseiten, im Hochsommer üppiger Graswuchs möglich war. Die Straßenböschungen und intensiv besonnte Dammabschnitte waren trockener und spärlicher bewachsen. Es wurden also mit den beiden Typen von Böschungen primäre bzw. sekundäre Lebensräume der Feldmaus im Sinne von STEIN (1956) verglichen.

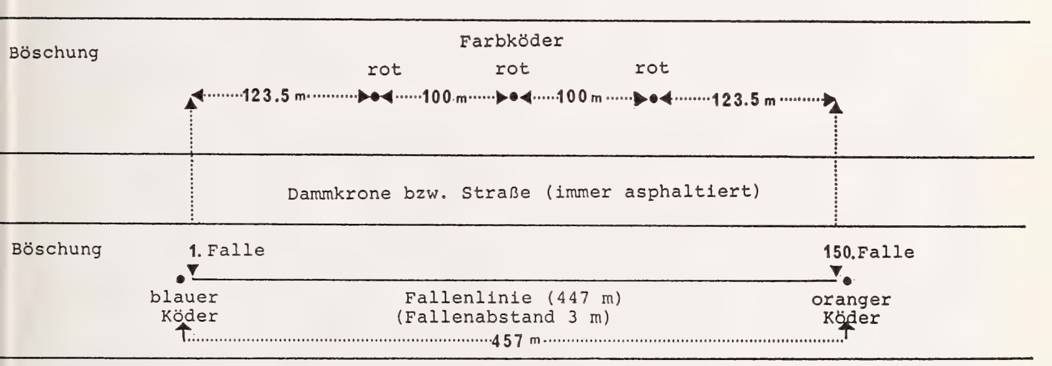


Abb. 1. Schema des Einsatzes von Fallen und verschiedenen Farbködern. Je Versuch wurde einmal eine Nord- und einmal eine Südseite mit Fallen versehen

Für die „Selbstmarkierung" der Tiere wurden nach den Empfehlungen von HOLIŠOVA (1968) farbige Wollfäden von 0,5 cm Länge in einem Anteil von 2 % des Ködergewichtes eingemischt. Farbechtheit der Wollfäden und Dauer des Verweilens im Darmtrakt sowie die Akzeptanz des Köders wurden vorher im Labor getestet. Als Ergebnis wurde Schmelzkäse verwendet. Wollfasern waren mittels Stereomikroskop bis zu 48 Stunden nachweisbar. Um ein Verschleppen von Ködern durch größere Tiere, wie es HOLIŠOVA (1968) berichtet, zu verhindern, wurde dieser in 30 cm langen PVC-Rohren mit lichter Weite von 4 cm, die waagrecht am Boden fixiert und verblendet wurden, angeboten. Auch die Eignung dieser Rohre wurde vor Beginn der Untersuchungen getestet. Am Tag

Tabelle 1. **Prozentanteile der markierten Männchen und Weibchen am Gesamtfang je Untersuchungsgebiet**

	Straßenböschungen (Marchfeld)		Dammböschungen (Au)	
	♂	♀	♂	♀
Gesamtfänge	142	241	92	89
Zahl mit Farbködern	11	21	2	5
%	7,7	8,7	2,2	5,6

vor dem Einsatz der Fallen wurden im Abstand von 457 m je ein Rohr mit blauem und orangem Köder ausgelegt. Auf der Gegenseite der Böschung kamen drei Rohre mit rotem Köder zum Einsatz. Am nächsten Tag wurden 150 Schlagfallen (3 m Abstand) zwischen den Ködern ausgebracht (Abb. 1) und mit Schmelzkäse oder Margarine beködert. Die Fallen waren 3 Tage und Nächte im Einsatz, d. h., jeder Versuch beruht auf je 150 Fallen an Nord- bzw. Südböschungen von Straßen und Damm; dies ergibt insgesamt 1800 Falleneinheiten je Monat.

Die gefangenen Tiere wurden einzeln und mit Datum, Fallennummer, Straßen- bzw. Dammseite etikettiert, tiefgekühlt für die Weiterverarbeitung gelagert. Bei der Sektion wurde nach der Erfassung der üblichen Daten geprüft, in welchem Darmabschnitt farbige Wollfäden vorhanden waren. Tab. 1 informiert über Gesamtfänge und Anzahl markierter Exemplare. Die Dichte war im Sommer 1987 leicht erhöht. Detaillierte Angaben finden sich bei Somsook (1990).

Ergebnisse

Die Fangdichte war von Jahreszeit und Bewirtschaftungseingriffen des Menschen abhängig (Somsook 1990). Darauf und auf Unterschiede zwischen Nord- und Südseite wird hier nicht eingegangen.

Der Anteil markierter ♀♀ ist mit 8,7 % (Straßen) bzw. 5,6 % (Damm) höher als der von ♂♂ (7,7 % bzw. 2,2 %) (Tab. 1).

Tab. 2 führt die zurückgelegten Mindestentfernungen an. Diese sind kleiner als die zumindest zurückgelegten Weglängen und entsprechen der Mindestlänge des Aktionsraumes. Bei Nachweis nur einer Köderfarbe gilt die Distanz zwischen Köderplatz und Fangort, bei Nachweis von zwei Farben die größte Distanz zwischen Köderplätzen bzw. Fangort als Mindestentfernung. Im Falle der Querung auf die andere Böschungsseite wurde angenommen, daß der Köder von der zunächst liegenden Stelle stammt. Die nachgewiesenen Mindestentfernungen variieren zwischen 8 und 457 m (Straße) bzw. 18 und 109 m (Damm). Ein Zusammenhang zwischen mittlerer Mindestentfernung und Gesamtdichte besteht nicht: die höchste durchschnittliche Entfernung wurde im Mai (geringe Dichte) erzielt, die beiden letzten Termine differieren zwar wenig in der Dichte, jedoch stark in der Entfernung (Straße). Monate mit sehr geringen Fängen (April) bzw. auch Mai, Juli und Anfang Oktober am Damm lieferten keine Wiederfänge; entscheidend war die Mahd am Damm, die die Tiere in Nachbarlebensräume vertrieb.

Tab. 3 zeigt, daß bei alleiniger Berücksichtigung des Mageninhaltes, wie dies z. B. bei Holišova (1968) und Andrzejewski und Babinska-Werka (1986) geschieht, ein Teil der Nachweise, vor allem diejenigen über 400 m Mindestentfernung, nicht erfolgt wäre.

Abb. 2 können Zusammenhänge zwischen Mindestentfernung, Geschlecht, Gewicht, Geschlechtsaktivität und Fangmonat entnommen werden. 25 Tiere liegen unter 100 m (64,1 %), 8 zwischen 100 und 200 m (20,5 %) und je zwei (je 5 %) in den nächsten drei

Tabelle 2. **Zurückgelegte Mindestentfernungen in einzelnen Fangperioden**

Fangzeiträume	Straßenböschungen					Dammböschungen				
	Gefangene Feldmäuse		Zurückgelegte Entfernungen (m)			Gefangene Feldmäuse		Zurückgelegte Entfernungen (m)		
	insgesamt	markiert	Min.	Max.	x̄	insgesamt	markiert	Min.	Max.	x̄
8.–10. 4. 87	11	–	–	–	–	–	–	–	–	–
13.–15. 5. 87	28	3	221	446	265,3	20	–	–	–	–
28.–30. 6. 87	29	1	18	18	–	71	5	18	109	56,4
29.–31. 7. 87	38	5	12	113	58,2	1	–	–	–	–
2.– 4. 9. 87	141	15	20	457	147,7	62	2	44	50	47,0
30. 9.–2. 10. 87	146	8	129	8	37,3	27	–	–	–	–
Summe/x̄	393	32	12	457	133,0	181	7	18	109	53,7

Tabelle 3. **Zusammenhänge zwischen zurückgelegter Mindestentfernung und Darmabschnitten, in denen Farbköder gefunden wurden**

Angegeben ist die Zahl positiver Fälle (mehrfach Nachweise je Individuum möglich)

Farbköder gefunden im	Mindestentfernung (m)									
	–50	–100	–150	–200	–250	–300	–350	–400	–450	–500
Magen	5	–	2	–	–	1	–	1	–	–
Dünndarm	6	3	6	–	1	–	1	–	–	2
Blinddarm	6	1	2	–	–	–	–	–	–	1
Enddarm	7	1	3	–	–	–	–	–	–	1
Insgesamt	24	5	13	–	1	1	1	1	–	4

100-m-Klassen. Der höchste nachgewiesene Wert von 457 m ist gleichzeitig der Maximalwert, der mit der Versuchsanordnung nachgewiesen werden könnte (vgl. Abb. 1). Aufschlußreich sind die Ergebnisse bezüglich Aktionsraum, Geschlecht und Fortpflanzungsaktivität: am weitesten bewegt haben sich drei laktierende ♀♀ von Mai bzw. September, von denen zwei gravide waren. Alle drei wurden in der ersten Fangnacht, also zwei Tage nach Ausbringen des Köders gefangen und hatten diesen in Magen oder Dünndarm. Die maximale Mindestentfernung bei ♂♂ sind 272 bzw. 323 m und betreffen inaktive Tiere vom 4. September. Geschlechtsaktive ♂♂ wurden nur dreimal markiert nachgewiesen: nur eines legte 221 m zurück, die beiden anderen weniger als 50 m!

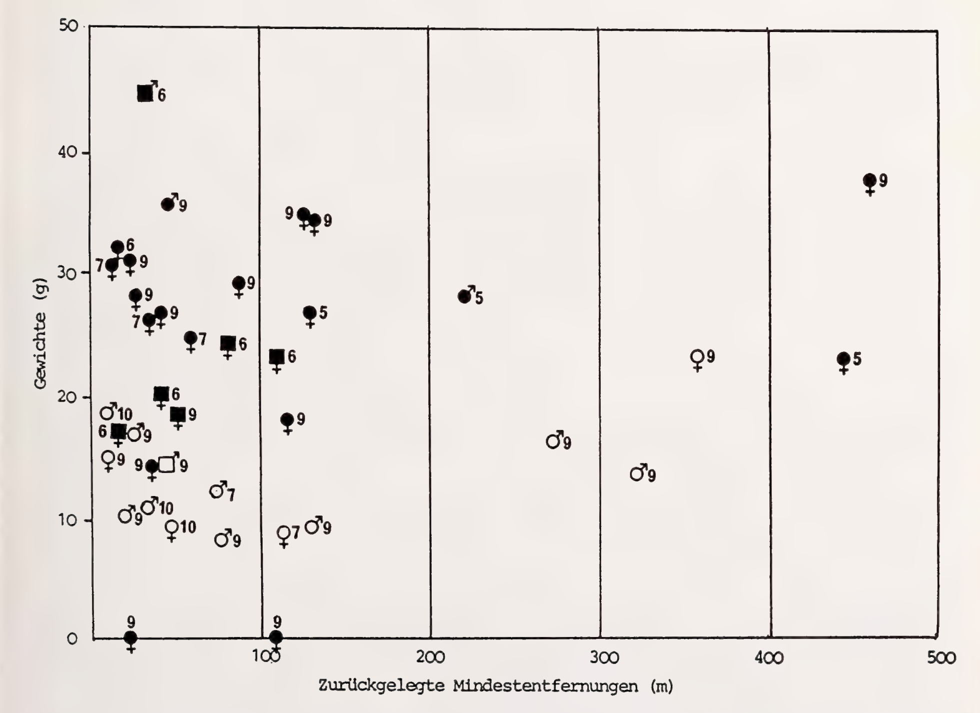


Abb. 2. Zusammenhänge von individuell zurückgelegter Mindestentfernung, Gewicht, Geschlechtsaktivität (ausgefüllte Symbole bedeuten geschlechtsaktiv) sowie Fangmonat (Zahlen). Runde Symbole beziehen sich auf die Straßenböschungen, quadratische auf die Dammböschungen (nicht mehr feststellbare Gewichte sind als „0 g“ angegeben)

Mit der Versuchsanordnung konnte auch ein Queren der Straße (5,5 m Breite, Verkehrsfrequenz sicherlich hunderte Fahrzeuge/Tag, keine genauen Zahlen verfügbar) bzw. der für Kraftfahrzeuge gesperrten Dammkrone (3 m breites Asphaltband, Radfahrverkehr) nachgewiesen werden. Beides stellte, auch in dem Jahr ohne Massenvermehrung, keine wesentliche Barriere dar: 45,4 % aller markierten ♂♂ bzw. 61,9 % der entsprechenden ♀♀ querten die Straße, und beide markierten ♂♂ bzw. 4 der 5 ♀♀ überschritten die Dammkrone. Die Nachweise verteilten sich ohne zeitliche Häufung auf den Untersuchungszeitraum. Der Anteil querender Tiere war bei den geschlechtsaktiven mit 65,4 % höher als bei den inaktiven mit 53,8 % (beide Geschlechter aus Materialgründen zusammengefaßt).

Diskussion

Nach den Untersuchungen von Andrzejewski und Babinska-Werka (1986) über die Rötelmäuse liegt hiermit eine weitere vor, die eine ähnliche Methode einsetzt und bei einer anderen Art, eben der Feldmaus, und in einem anderen Lebensraum, nämlich begrasten Böschungen, zu entsprechenden Ergebnissen gelangt. Bei der zitierten Untersuchung hätten vielleicht Haferkörner verschleppt und dann auch von anderen Individuen genutzt werden können. Um dies auszuschließen, wurde von uns Schmelzkäse mit beigemischten Wollfasern verwendet. Dies hat auch den Vorteil, daß verschiedene Farben eingesetzt werden können, was einen präziseren Nachweis der Köderherkunft erlaubt. Zur Verhinderung der Fehlermöglichkeit des Verschleppens ganzer Köderkuchen (vgl. Holišova 1968) haben wir den Köder, unzugänglich für größere Tiere, in Rohren angeboten. Die dadurch verringerte Geruchsausbreitung bedingte einen bedeutend geringeren Anteil markiert gefangener Individuen: 6,9 % gegenüber 92 %. Auch die mit nur einem Tag gedrittelte Anköderzeit wirkte sicherlich im gleichen Sinne. Wir wollten dadurch die Gewöhnung an die zusätzliche Nahrungsquelle ausschließen.

Andrzejewski und Babinska-Werka (1986) haben ihr Experiment nur einmal, im Juli, durchgeführt, wir hingegen sechsmal, verteilt auf das Sommerhalbjahr. Die durch Bewirtschaftungseinflüsse sehr gestörten Verhältnisse in unserem Untersuchungsgebiet erlauben jedoch keine Betrachtung jahreszeitlicher Dynamik. Ferner ist unsere Untersuchung in Lebensräumen „linearer“ Struktur durchgeführt worden, nicht wie in Polen in einem großen, recht homogenen Wald. Trotz all dieser Unterschiede sind die Ergebnisse von prinzipiell großer Übereinstimmung: wie bei den Rötelmäusen in Polen hätte auch mit unserer Versuchsanordnung keine höhere Mobilität nachgewiesen werden können, als es mit 285 bzw. 457 m für fortpflanzungsaktive Feldmaus-♀♀ tatsächlich gelang. Die Männchen der Rötelmäuse in Polen hatten größere Aktionsräume als unsere Feldmaus-♂♂. Der bisher bei Microtiden als gesichert angesehene Geschlechtsunterschied im Raum-Zeit-Verhalten (♀♀ mit kleineren Aktionsräumen als ♂♂) wurde also in beiden Untersuchungen nicht bestätigt: Fortpflanzungsaktive ♀♀ sind mobiler als aktive ♂♂, besonders bei der Feldmaus! In beiden Fällen wurden die im Experiment maximal nachweisbaren Mindestdistanzen von der jeweils untersuchten Art zurückgelegt. Dies fordert noch längere Versuchslinien, welche von Mitarbeitern von Andrzejewski mittlerweile auch eingerichtet worden sind (pers. Mitt. an Steiner) und noch höhere Mobilität nachweisen. Dementsprechend und in unserem Falle auch der Längserstreckung der untersuchten Böschungen wegen, halten wir weiterreichende und detailliertere Überlegungen über die Aktionsräume für verfrüht. Es kann aber als gesichert gelten, daß diese um mehr als eine Zehnerpotenz größer sind, als bisher angenommen wurde.

Damit verbunden ist die Frage der Überlappung von Aktionsräumen auch bei den oft als territorial angesehenen ♀♀. Gerade in linearen Lebensräumen muß es bei beträchtlicher Aktionsraumgröße zu einer sehr starken Überlagerung derselben kommen.

Wir konnten auch untersuchen, wie häufig Feldmäuse eine Straße bzw. eine 3 m breite

asphaltierte Dammkrone (tagsüber Radfahrverkehr) überquerten. Nachdem mehr als die Hälfte der markierten Tiere über die Verkehrsflächen wechselten obwohl keine überhöhte Dichte herrschte, kann gesagt werden, daß für die Feldmaus – anders als z. B. für waldlebende Gelbhalsmäuse *Apodemus flavicollis* (Melchior, 1834), vgl. Mader und Pauritsch (1981) – Verkehrsflächen praktisch kaum Barrieren darstellen.

Sicherlich müssen die Ergebnisse der Populationsanalysen auf Flächen, die von einem Fallenraster bedeckt waren und wo die Tiere die Fallenorte aus längerer Erfahrung kannten, mehr oder minder verworfen werden. Die Feststellung von Reichstein (1960) bezüglich der Flächenmethode („In welcher Größenordnung der tatsächliche Aktionsraum liegt, läßt sich auf diesem Wege nicht ermitteln") hat in diesem Lichte großen Weitblick bewiesen, ging aber in der Folge unter, auch bei seinen eigenen weiteren Überlegungen.

Unsere Resultate stützen die Kritik der zitierten polnischen Autoren an den Flächenmethoden. Sie können jedoch darüber hinaus keine endgültigen Antworten auf die Frage der Aktionsraumgröße der Feldmaus geben. Diese sind aber sicher wesentlich höher als derzeit angenommen (Niethammer und Krapp 1982) und überlagern sich zu einem großen Teil. Fallenlinien haben daher sicherlich einen höheren Einzugsbereich, als allgemein akzeptiert wird, deshalb müssen ihre Fänge auf größere Flächen bezogen werden – außer eine Art ist streng an bestimmte und nur kleinräumig vorhandene Strukturen gebunden. Es ergibt sich die Notwendigkeit zu weiteren Experimenten, z. B. Ausfang von fluchtsicher umgrenzten Flächen, wie ihn Dieterlen (1967) durchgeführt hat.

Danksagung

Für tatkräftige Hilfe bei der Feldarbeit danken wir den Herren Helmut Götz, Harald Kutzenberger, Dr. Manfred Pintar, Anton Reiter und Florian Steiner. Die Österreichische Wasserstraßendirektion (Dipl.-Ing. Hans Wösendorfer) förderte die Studie bezüglich des Hochwasserschutzdammes. Mr. John Reid und Frau Dr. Susanne Schnack halfen bei der Erstellung des Abstract. Für die vielfältige Hilfe danken wir sehr herzlich.

Zusammenfassung

An Böschungen von Straßen im Kulturland östlich Wiens bzw. des Hochwasserschutzdammes der südlich angrenzenden Donau-Auen wurde mit farbigen Wollfäden vermischter Schmelzkäse als Köder in liegenden Plastikröhren angeboten. In den nächsten 3 Tagen kamen 4 Linien zu je 150 Fallen in 447 m langen Geraden zum Einsatz. Diese Experimente wurden im Sommer 1987, einem Jahr leicht erhöhter Dichte von *Microtus arvalis*, in monatlichen Abständen und immer an neuen Stellen, sechsmal durchgeführt.

Im Darm erbeuteter Feldmäuse gefundene Wollfasern beweisen, daß deren Aktionsräume mindestens um eine Zehnerpotenz größer sind, als nach Experimenten mit auf kleinen Probeflächen individuell markierten Tieren zu erwarten war: Gravide und laktierende ♀♀ bewegten sich bis zu 457 m, ♂♂ mit über 300 m etwas weniger weit. Diese Befunde stehen in großer prinzipieller Übereinstimmung mit denen von Andrzejewski und Babinska-Werka (1986) an Rötelmäusen polnischer Wälder. Unsere Feldmäuse haben asphaltierte Straßen regelmäßig überquert.

Weitere Experimente mit noch längeren Fallenlinien werden genauere Einblicke geben. Allgemein haben Fallenlinien sicherlich weitere Einzugsbereiche, als man bisher annahm.

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Social relations and individual coping reactions in a captive group of Central American Agoutis *(Dasyprocta punctata)*

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Abstract

Studied a captive group of Central American agoutis *(Dasyprocta punctata)*, consisting of 20 animals. The study focusses on relationships and individual coping reactions of six females, living together in unusually close proximity without all of them realizing an exclusive pair-bond to a male. Group structure centred on the pair-bond between the adult male and the oldest female (F1). F1 and her adult daughter (F3) were mutually attached. Another adult daughter of F1 (F2) displayed excessive maternal behaviour towards own and other young. F2, an introduced adult female (F4) and subadult daughters of F1 and F2 showed no enduring social attachment. For the non-attached females the frequencies of some agonistic and arousal-indicating behavioural elements were correlated with their monthly indices of retreat in relation to specific females indicating specific activations of aggression accompanied by specific levels and states of arousal. The hypothesis is proposed, that the females developed the different individual reactions by activating portions of their behavioural and motivational programmes, occasionally in excess, in coping with their specific situation to such an extent, that stress could be held low or moderate and regular breeding remained possible.

Introduction

Agoutis (*Dasyprocta* sp.), which are described in the field as living as monogamous pairs in defended areas (Smythe 1978; Dubost 1988) can, in captivity, be held in larger groups in which several females breed regularly without the possibility for all of them to develop an exclusive attachment to a male.

Bowlby (1969) regarded attachment as a behavioural system with its own form of internal organisation. Attachment in ethology is understood as the result of a process within the attached individuals, which activates specific possibilities of the behavioural programme and promotes an internal state of security (cf. Wickler 1976; Hendrichs 1978; Bischof 1985). It seems useful to differentiate between the transient mother-young attachment and the long-lasting bonds between adult animals (Bischof 1985; Hendrichs 1988). Depending on the qualities of social bonds, agoutis can activate different behavioural patterns and systems in regulating social situations and internal states (Korz and Hendrichs 1989). A central variable of internal dynamic is arousal, which can be differentiated at the levels of general arousal and specific states of arousal. Arousal can be correlated with qualities and frequencies of specific behavioural elements, e.g. scent-marking or autogrooming (cf. Ralls 1971; Eisenberg and Kleiman 1972). Specific behavioural indicators and correlations for the agouti are described by Korz and Hendrichs (1989). In group-housed females of the closely related acouchi *(Myoprocta pratti)* Kleiman (1972) found comparable results: positive correlations between frequencies of autogrooming and chasing as well as food-burying and higher frequencies of autogrooming in group-living than in isolated females; she discusses this as an outcome of social stress. Social stress can be regarded as a consequence of escalated and long-lasting arousal through frequent social perceptions (Hendrichs 1978).

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In a territorial and monogamous species, pair-bond and territorial ownership are related to dominance (cf. KLEIMAN 1977), social bonds reducing aggression between bonded animals and often increasing aggression towards conspecifics (cf. EISENBERG 1966). Aggression in the sense of agonistic behaviour, however, is not necessarily correlated with the dominance state of an animal (ROWELL 1974; HAND 1986; FRANCIS 1988).

Thus, the primary aim of the present study was to characterise the specific social and dominance relations of the females in the observed group and to assess, in which way the individual females adjust to living together in a situation without exclusive use of space, in unusually close proximity to other females and especially most of them without realizing an exclusive pair-bond to a male. Besides contributing to a better understanding of the behavioural qualities of the agouti, such studies can further our knowledge on mechanisms and functions of social attachment.

Material and methods

Animals

Central American agoutis, descendants of animals captured in Guatemala, have been bred at the University of Bielefeld, Department of Ethology since 1974. From April 1985 to December 1986 one group of 20 animals was observed, quantitative behavioural data were recorded from June 1985 to July 1986. At the beginning of observation the group consisted of 1 adult male (M1, 10 years old), 4 adult females (cf. Fig. 1), 2 subadult females (F12, F31 each one year old), 1 subadult male (removed at 9. 8. 1985), 1 male and 3 female young. F1 is the mother of F31, F3 and F2; F2 is the mother of F12. F4 was born in another group and introduced to the group in 1982; she died in November 1986. M1 is the father of F1, F2, F3, F31, F12 and of all young. He belongs to the first generation born in Bielefeld and died in February 1986. The six adult and subadult females were the subject of the present study. Females have a post-partum-estrus lasting a few hours; the estrus cycle has a length of 34–36 days (cf. WEIR 1971 for *Dasyprocta aguti*, own observation). Pregnancy lasts about 115–120 days. The one or two pups are well developed and begin to feed on their own at an age of two weeks, although they can suckle up to an age of three months. Sexual maturity is achieved at an age of six months. With four to five months of age immature animals were chased by adults (particularly by their mothers) for two to three months; thereafter the frequencies of chasing decreased.

The animals were kept in an outdoor enclosure of 9.00 m × 4.65 m, subdivided by wire-mesh into four parallel compartments of identical size connected by passages 0.75 m in width. Three of the compartments were each connected with a wooden sleeping cabin (1.10 m × 1.75 m) outside the enclosure; the fourth compartment had a smaller cabin (0.80 m × 0.70 m). The ground consisted of gravel covered with sand. The enclosure contained two wooden chests and branches. The ambient temperature varied from +30 °C to −10 °C. In winter the enclosure was protected against snow and coldness by partly transparent canvas; the larger sleeping cabins contained heat-lamps. The animals were fed corn, rolled oats, fresh vegetables, fruits and leaves once a day (dry food and water ad libitum). Three of the sections had a food-bowl, only two of them water-bowls.

Data recording and analysis

The behaviour of all animals was recorded by written entries in one-minute intervals as scan samples at those times of day (6–12 a.m., 17–21 p.m.) when all animals of the group were active. The analysis takes into account 150 hours of behavioural protocols. An index of retreat was computed for each two females based on the ratio $RI = R^+ / R^+ + R^-$ (R^+: number of retreats displayed by female A in reaction to a specific female B, R^-: number of retreats shown by female B in reaction to female A). Numbers of retreats are based on all recorded encounters between females ending with a retreat of one or both. The higher this index (ranging from 0–1) is for one of the two females, the clearer her superiority is regarded to be in relation to the other. The level of significance for all statistical tests (cf. figure and table legends) is $< = 0.05$.

A preference was defined a) for males if a male directed more than twice as much courtship behaviour towards one specific female than he showed on average towards every female (cf. SACHSER 1986 for guinea pigs), b) between females if a female directed more than twice as much contact behaviour towards one female as she showed on average towards every female.

The following behavioural elements were recorded: "Bury": The animal takes a piece of food in its mouth, digs a hole into the ground with its forefeet, places the piece of food in the hole and covers it

up, pressing the substrate with the forefeet. "Scrape": The animal scrapes the ground with its forefeet (can change into burying and vice versa). "Nibble-of-bodysides": The animal nibbles at its flanks. "Scratch": The animal scratches its flanks with its hind leg turning its body. "Lick": The animal raises a forefoot and licks it. "Tremble": Brief body-trembling with hair erected. "Scentmark": The animal

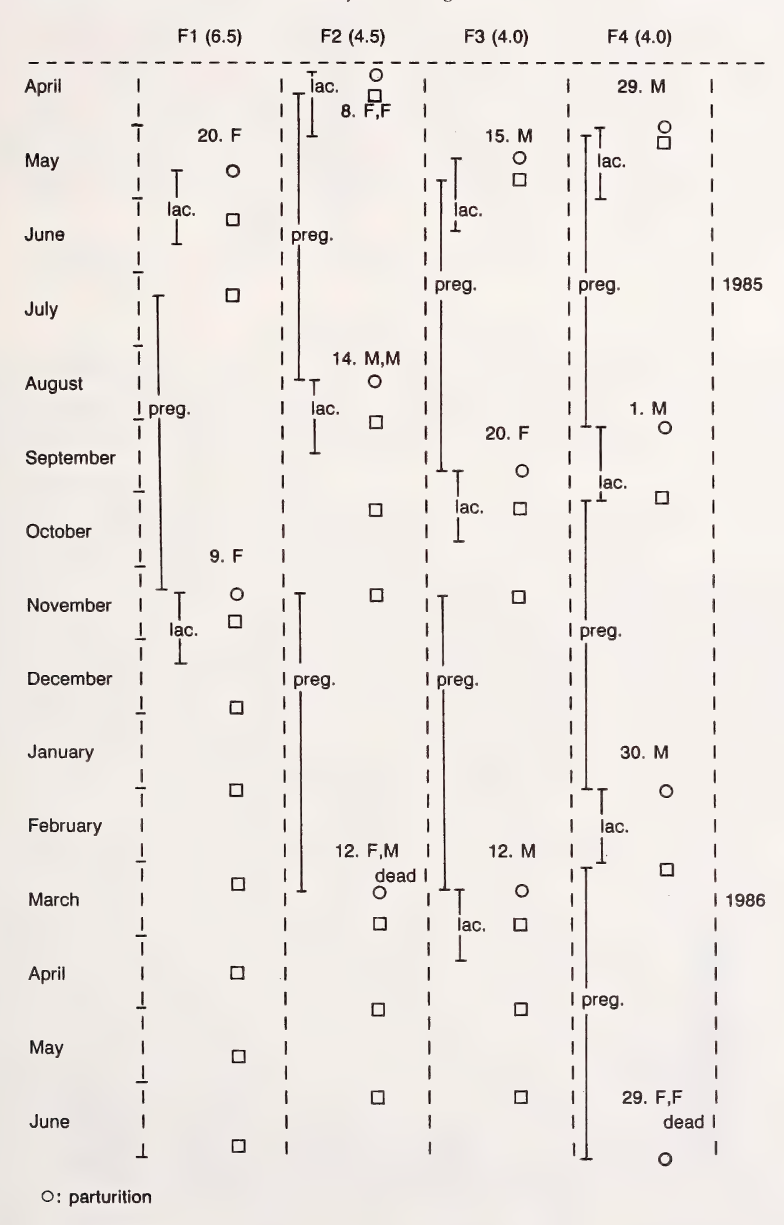


Fig. 1. Reproductive states of the adult females during period of observation. Numbers in brackets give the age of females (in years) at the beginning of data recording. Numbers give the dates of parturition (F = female young, M = male young), vertical lines label spaces of time, lac = lactation (period of regular suckling), preg = pregnancy

drags its anal glands over the ground leaving a secretion. "Chase": The animal runs after another one for at least two meters. "Joust": Standing opposite on their hind legs two animals drum on each other with their forelegs. This behaviour is often accompanied by raising the rump hair. "Head-thrust": The animal thrust its raised head at another. "Head-raise": Standing in front of or parallel to another animal at a distance of up to one meter the animal having raised its head stares at the other. "Bite-attempt": A biting movement in the direction of another animal while sitting, standing or quickly approaching. "Nuzzle": The animal nuzzles the corner of another's mouth (mostly when this one has a piece of food in its mouth). "Nibble": The animal sits at the side of another nibbling the region from ear to corner of the mouth of the other's head. "Sniff": The animal sniffs at parts of another's body. "Chin-raise": A male approaches a female with raised chin. "Drive": A male follows a female with raised chin for at least two meters. "Urine-spray": A male approaches a female, raises its body, and sprays a jet of urine in the direction of the female. "Follow": A male follows a female in a distance up to two meters. "Anal-licking": A female licks the anal region of a young. "Spit": A sound that females can display when a male approaches.

Results

Male-female relationships

M1 shows a preference for F1 (cf. Fig. 2). The amount of "Follow" is three times as high as the average amount towards every female. Referred to the adult females, "Nibble" occurred exclusively between M1 and F1 (the one "Nibble" towards F31 can be explained by the age of this female, "Nibble" occurring frequently between adult and young animals). On the whole M1 directed 50.2 % of the recorded behaviour towards F1. Fig. 1 gives the changes of some reproductive states of the four adult females from April 1985 to February 1986. Estrus of females (because of its short space of time) is difficult to observe directly, therefore the estrus-dates in Fig. 1 were computed proceeding from dates of parturitions with a scope of three days before and after the approximate dates of estrus. The frequency of "Nibble" M1 directed towards F1 was 0.80/h (18.6 h of observation) around estrus and 0.37/h (101.4 h of observation) out of estrus. Frequencies of courtship behaviour around estrus M1 directed towards F1 were 0.59/h, towards F2 0.00/h (7.7 h of observation), towards F3 0.81/h (3.7 h of observation) and towards F4 0.00/h (2.5 h of observation); frequencies out of estrus were 0.49/h towards F1, 0.09/h (112.3 h of observation) towards F2, 0.10/h (116.3 h of observation) towards F3 and 0.15/h (117.5 h of observation) towards F4. Fourteen days before and after parturitions, no remarkable

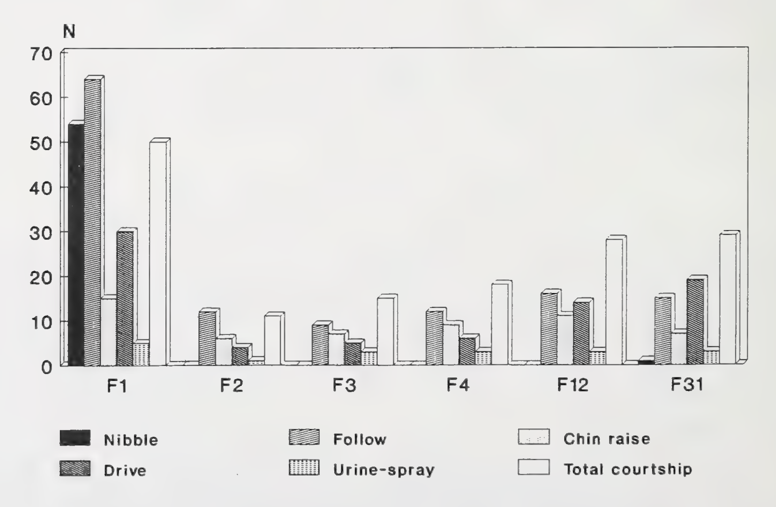


Fig. 2. Amounts of "Nibble", "Follow" and courtship behaviour that the male M1 directed towards the females from June 1985 to January 1986 (120 h of observation)

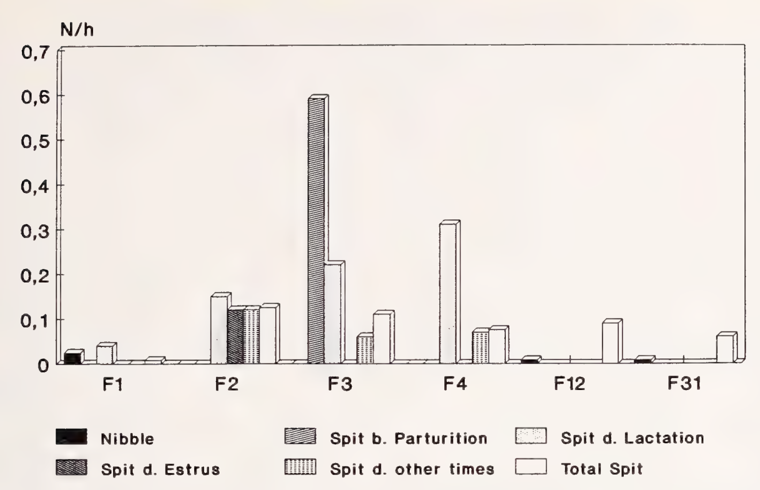


Fig. 3. Frequencies of "Nibble" and "Spit" that the females directed towards the male M1 from June 1985 to January 1986. b = before (14 days), d = during. N/h = average amount of behavioural element per hour

changes in frequencies of courtship behaviour appeared, but F1 was the only female courted by M1 in this period after parturition.

The frequency of the threat behaviour "Spit" directed to M1 is distinctly lower in F1 than in the other females (Fig. 3). "Spit" mainly occurred in periods of lactation with the exception of F3 which spat mostly in the fourteen days before parturition. The one "Spit" of F1 occurred shortly after parturition. F2, F3 and F4 also spat when they were not in a striking reproductive state. Agonistic behaviour of M1 towards females only occurred in few cases towards the subadult ones.

Female-female relationships

The amounts and distribution of agonistic (Table 1) and of contact behaviour (Table 2) show distinct differences between the females. Agonistic behaviour of F1 was mainly directed towards F2 and F12, that of F2 predominantly towards F1, the amounts directed towards the other females still being relatively high. F2 directed 40.3 % of her total amount of agonistic behaviour (268) towards F1, while F1 directed 52.9 % from a total of 202 towards F2. The main behavioural element which occurred between these females was "Joust". The main element of agonistic behaviour that F1 directed towards F12 was "Chase". F3 and F4 mostly directed agonistic behaviour towards F2 and F12. F12 showed agonistic behaviour, especially "Chase", mostly towards F2; F31 mostly towards F12. F2 displayed "Joust" more frequently (44.8 % from a total of 268) than any of the other females (F1 38.1 %, F3 11.3 %, F4 22.7 %, F12 25.2 % and F31 11.4 %) showing 66.6 % of this behaviour in 50 days following parturitions.

Preferences in directing contact behaviour are only recognisable between F1 and F3, and for F12 towards F1. Although following the definition, the amounts of contact behaviour shown by F2 towards F4 and by F4 and F31 towards F3 are too small to evaluate a preference. Between F3 and F1 "Nibble" occurred frequently and exclusively (with the exception of one "Nibble" of F1 towards F4). F2 and F12 did not display "Nibble" and among the other females, "Nibble" occurred infrequently. The distribution of agonistic and contact behaviour did not change after the death of M1.

Table 3 gives the monthly RIs for female pairs. The RIs of F2 towards any of the other

Table 1. **Amounts of agonistic behaviour between the females**

		F1	F2	F3	F4	F12	F31
F1	CH		14	0	2	33	2
	JO		61	0	9	5	2
	HT		3	0	0	4	0
	HR		15	1	3	13	3
	BA		14	1	1	13	3
	Total		107	2	15	68	10: 202
F2	CH	4		4	6	10	6
	JO	67		7	22	15	9
	HT	4		1	3	2	2
	HR	20		10	7	8	13
	BA	13		10	5	13	7
	Total	108		32	43	48	37: 268
F3	CH	0	3		0	11	0
	JO	0	7		2	0	0
	HT	1	3		1	2	0
	HR	0	10		0	11	2
	BA	3	5		1	17	0
	Total	4	28		4	41	2: 79
F4	CH	1	27	0		5	1
	JO	8	21	1		5	0
	HT	0	10	0		2	0
	HR	1	25	0		10	1
	BA	3	8	0		20	5
	Total	13	91	1		42	7: 154
F12	CH	0	37	0	0		1
	JO	2	16	0	4		5
	HT	0	3	0	0		1
	HR	0	18	0	2		1
	BA	1	11	1	1		3
	Total	3	85	1	7		11: 107
F31	CH	0	1	0	6	60	
	JO	2	8	0	0	10	
	HT	0	1	0	0	6	
	HR	0	3	1	3	9	
	BA	0	5	2	13	46	
	Total	2	18	3	22	131	: 176

CH = "Chase", JO = "Joust", HT = "Head-thrust", HR = "Head-raise", BA = "Bite-attempt". Amounts in 150 h of observation, behaviour of females on left side directed towards females above

females increased in August/September and in March/April, which were the months of parturition and lactation of F2 (cf. Fig. 1). In these periods her relations of superiority became unstable especially towards F1 and F3. Such a correlation is not found in the other females. Between estrus-dates and changes in RIs, no correlation is obvious in any female.

The monthly frequencies of "Chase", "Head-thrust" and "Bite-attempt" that F4 displayed towards F2 are positively correlated with her monthly RIs (cf. Table 4). The frequencies of "Bite-attempt" that F2 and F31 directed towards F12 and the frequencies of "Chase" F12 displayed towards F2 are correlated with their respective RIs. In the case of F2 the correlation depends on a rise in frequencies of agonistic behaviour and RIs towards F12 in the months of parturition and lactation. No significant correlations occur between frequencies of agonistic elements and RIs in F1 and F3 towards any other female. The frequencies of "Bury", "Scrape", "Nibble-of-bodysides", "Scratch", "Lick", "Tremble"

Table 2. **Amounts of contact behaviour between the females**

		F1	F2	F3	F4	F12	F31
F1	NU		0	20	1	3	0
	NI		0	5	1	0	0
	SN		1	1	0	1	3
Total			1	26	2	4	3: 36
F2	NU	0		0	3	0	0
	NI	0		0	0	0	0
	SN	1		2	1	0	0
Total		1		2	4	0	0: 7
F3	NU	34	0		0	0	2
	NI	11	0		0	0	0
	SN	12	1		1	1	1
Total		57	1		1	1	3: 63
F4	NU	1	0	5		0	0
	NI	1	0	0		0	0
	SN	2	2	1		0	0
Total		4	2	6		0	0: 12
F12	NU	13	2	7	2		0
	NI	0	0	0	0		0
	SN	3	4	1	4		1
Total		16	6	8	6		1: 37
F31	NU	5	3	7	0	0	
	NI	0	1	2	1	0	
	SN	0	0	0	0	0	
Total		5	4	9	1	0	: 19

NU = "Nuzzle", NI = "Nibble", SN = "Sniff". Amounts in 150 h of observation, behaviour of females on left side directed towards females above.

and "Scentmark" can be taken as indicators of arousal of the animals (cf. Korz and Hendrichs 1989). The higher the frequency the more the animal is aroused. By multivariate analysis (correspondence analysis) of occurring frequencies these behavioural elements are ordered along an "axis of intensity", decreasing from "Bury" to "Tremble", the elements indicating different states of arousal. Frequencies of the less intense behaviour "Lick", "Nibble-of-bodysides" and "Tremble" of F2 correlate with the RIs towards F1, F3 and F4 (cf. Table 5). Frequencies of the less intense behaviour "Lick" of F12 correlate with the RIs towards F2. Frequencies of "Lick", "Nibble-of-bodysides" and the more intense behaviour "Scrape" of F31 correlate with the RIs towards F12. All correlation coefficients of behaviour of F4 are negative, the high intense behaviour "Bury" significantly correlating with RIs towards F2. There are no significant correlations of behavioural elements in F1 and F3.

Female-young relationships

Concerning maternal behaviour towards own and other young (up to an age of six months) F2 was of marked individuality, the amount of "Anal-licking"/ young is more than thrice as high (6.75) as the second-highest frequency towards own young (2.00, F1) and nearly ten times as high (5.40) as the second-highest frequency towards other young (0.56, F4). The relatively high frequencies of "Anal-licking" in the subadult females F12 (1.20) and F31 (2.90) probably result from play-like behaviour; these females are inexperienced yet in raising their own young. The frequency of "Chase" (2.18) and "Bite-attempt" (5.55) that F2 displayed towards young other than her own is the lowest of all females, ranging from

Table 3. **Indices of retreat for the pairs of females**

	F1/F2	F2/F1	F1/F12	F12/F1	F2/F3	F3/F2	F2/F4
June	0.87	0.13	1.00	0.00	0.13	0.87	0.04
July	0.82	0.18	0.90	0.10	0.13	0.87	0.04
August	0.35	0.65	1.00	0.00	1.00	0.00	0.80
September	0.47	0.53	1.00	0.00	0.85	0.15	0.08
October	0.00	1.00	–	–	0.50	0.50	0.10
November	–	–	–	–	–	–	–
December	0.50	0.50	–	–	–	–	0.08
January	–	–	–	–	–	–	–
February	–	–	–	–	–	–	–
March	0.56	0.44	0.92	0.18	0.85	0.15	0.83
April	0.40	0.60	1.00	0.00	0.84	0.16	0.83
May	0.85	0.15	1.00	0.00	0.20	0.80	–
June	0.33	0.67	1.00	0.00	0.00	1.00	0.62

	F4/F2	F2/F12	F12/F2	F4/F12	F12/F4	F12/F31	F31/F12
June	0.96	0.61	0.39	1.00	0.00	0.04	0.96
July	0.96	0.00	1.00	1.00	0.00	0.00	1.00
August	0.20	0.60	0.40	0.80	0.20	0.10	0.90
September	0.92	0.50	0.50	–	–	0.00	1.00
October	0.90	0.37	0.63	–	–	0.00	1.00
November	–	0.00	1.00	–	–	0.00	1.00
December	0.92	0.00	1.00	1.00	0.00	–	–
January	–	–	–	–	–	–	–
February	–	–	–	1.00	0.00	–	–
March	0.17	0.43	0.57	–	–	0.00	1.00
April	0.17	0.09	0.91	0.25	0.75	0.00	1.00
May	–	0.00	1.00	–	–	0.00	1.00
June	0.38	0.00	1.00	–	–	0.00	1.00

The indices refer to the first specified female. For less than five retreats no index was computed (–). Pairs of females with less than six indices were not taken into account.

2.49 (F4) to 15.40 (F1) of "Chase" and from 5.78 (F4) to 8.63 (F12) of "Bite-attempt". In all females the frequencies of "Nibble" were higher towards own (F1: 7.50, F2: 8.25, F3: 4.00 and F4: 5.00) than towards other young (F1: 0.75, F2: 1.20, F3: 0.25 and F4: 1.70). Figure 4 shows the frequencies of all agonistic and contact behaviour that the females directed towards young. F2 displayed significantly more contact behaviour towards young other than her own than any of the other adult females, and she is the only female displaying more contact than agonistic behaviour towards other young. Towards own young F2 showed significantly more contact behaviour than F3 and F4 (Fig. 4). Regarding all young, F2 displayed significantly more contact behaviour (76.20/y) than F1 (47.20/y), $Chi^2 = 6.82$, $p < 0.01$); F3 (17.50/y, $Chi^2 = 36.77$, $p < 0.001$) and F4 (23.20/y, $Chi^2 = 28.26$, $p < 0.001$); (Chi^2-test, two-tailed, df = 1).

Discussion

The preference of M1 for F1 (cf. Fig. 2) and the nearly whole absence of threat behaviour of F1 towards M1 (cf. Fig. 3) point to a specific relationship. The exclusive occurrence of "Nibble" between M1 and F1 in addition indicates a pair-bond, not restricted to times of estrus. Lamprecht (1973) and Wickler (1976) demand the exclusive occurrence of at least one behaviour restriced to pair members. Smythe (1978) in the field observed mutual

Table 4. **Correlation coefficients for the monthly indices of retreat and frequencies of agonistic behavioural elements between the females**

	F1/F2 N = 10	F1/F12 N = 8	F2/F1 N = 10	F2/F3 N = 9	F2/F4 N = 9	F2/F12 N = 9
CH	0.21	−0.09	–	–	–	–
JO	−0.27	–	0.43	0.25	0.07	0.19
HT	0.05	–	–	–	–	–
HR	−0.07	−0.15	0.54	0.63	0.12	–
BA	0.15	0.26	0.27	0.51	0.25	0.78***

	F3/F2 N = 9	F4/F2 N = 9	F4/F12 N = 6	F12/F2 N = 11	F31/F12 N = 10
CH	–	0.89***	−0.35	0.67**	0.06
JO	−0.23	−0.11	–	−0.19	0.38
HT	–	0.69*	–	–	0.21
HR	0.52	0.21	0.48	0.50	0.33
BA	0.43	0.75**	0.30	0.31	0.68*

CH = "Chase", JO = "Joust", HT = "Head-thrust", HR = "Head-raise", BA = "Bite-attempt". Spearman-rank-correlation-test (two-tailed); *: $p < 0.05$, **: $p < 0.02$, ***: $p < 0.01$. For less than four monthly frequencies of behaviour other than zero no coefficient was computed. Coefficients refer to the first specified female. Frequency: average amount of behavioural element per hour.

Table 5. **Correlation coefficients for the monthly indices of retreat and frequencies of behavioural elements indicating arousal**

	F1/F2 N = 10	F1/F12 N = 8	F2/F1 N = 10	F2/F3 N = 9	F2/F4 N = 9	F2/F12 N = 9
BU	−0.20	0.20	0.26	0.42	−0.38	0.28
SP	−0.30	0.26	0.30	−0.36	−0.30	−0.27
SC	−0.08	0.15	0.30	0.06	0.37	0.20
NB	−0.26	0.07	0.43	0.69**	0.67*	0.25
LI	0.03	0.15	0.63*	0.10	0.50	−0.04
TR	−0.13	0.03	0.51	0.44	0.67*	0.01
SM	−0.16	0.32	−0.06	−0.17	−0.11	−0.23

	F3/F2 N = 9	F4/F2 N = 9	F4/F12 N = 6	F12/F2 N = 11	F31/F12 N = 10
BU	0.48	−0.63 p=0.06	−0.85***	−0.12	−0.33
SP	0.42	−0.37	−0.33	0.56 p=0.07	0.62 p=0.05
SC	−0.21	−0.19	−0.68	0.11	0.51
NB	0.31	−0.59 p=0.09	−0.51	0.53 p=0.09	0.68***
LI	0.41	−0.25	−0.33	0.69 p=0.01	0.62 p=0.05
TR	−0.06	−0.19	−0.33	0.25	0.52
SM	0.29	−0.19	−0.33	0.42	0.00

BU = "Bury", SP = "Scrape", SC = "Scratch", NB = "Nibble-of-bodysides", LI = "Lick", TR = "Tremble", SM = "Scentmarking". Spearman-rank-correlation-test (two-tailed); *: $p < 0.05$, **: 0.04, ***: $p < 0.03$. Coefficients refer to the first specified female. Frequency: average amount of behavioural element per hour.

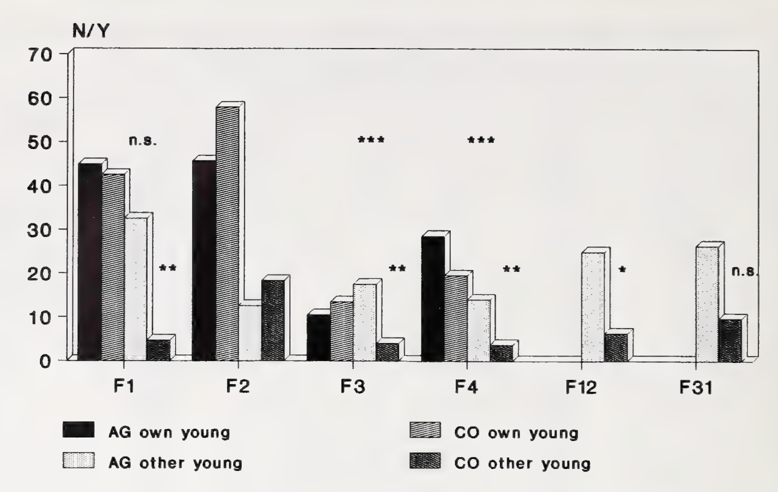


Fig. 4. Frequencies of agonistic and contact behaviour (including "Following in close distance" and "Retrieving") the females directed towards own and towards other young (frequency: average amount of behaviour per young). AG own young: agonistic behaviour towards own young, CO own young: contact behaviour towards own young, AG other young: agonistic behaviour towards other young, CO other young: contact behaviour towards other young. The statistical tests for the frequencies of contact behaviour of the specific females refer to the frequencies of F2. For own young: Chi^2-test (two-tailed, df = 1): * $p < 0.02$, ** $p < 0.01$, *** $p < 0.001$; for other young: Binomial test (two-tailed): * $p < 0.02$, ** $p < 0.01$

grooming of the ear region only in paired agoutis. This behaviour probably corresponds to "Nibble" described here. In addition to the preferences of F1 and F3 for each other (cf. Table 2) the existence of a mutual attachment is indicated by the nearly exclusive occurrence of "Nibble" with regard to the nearly complete absence of this behaviour between the other females (Table 2). It is assumed that, after the phase of expulsion of immature animals, females no longer recognise the young animals as their offspring. Smythe (1978) observed that both sexes harass any subadult they meet, even the progeny of adjacent territory-holders on their parents' territories. Nevertheless the attachment between F1 and F3 may be attributed to an enduring activation of components of mother-young-attachment.

The exaggerated display of maternal behaviour of F2 extended to young other than her own (cf. Fig. 4) points to a readily activated maternal state in this female, going along with higher frequencies of agonistic behaviour towards the other females. F2, F31, F12 and especially F4 enforced retreat of other females by agonistic efforts. F4 employed higher escalated agonistic behaviour ("Chase" and "Head-thrust") towards F2. Similar to F12 ("Chase") (cf. Table 4), F31 uses less escalated agonistic behaviour ("Bite-attempt") towards F12.

These different social relations and reactions can be seen as specific activations of motivational and behavioural programmes, which enable the females to cope with their specific social situation. In addition to the different relations and reactions, the females showed different levels and states of arousal. F2, F12 and F31 were aroused more and specifically in their efforts to gain and maintain superiority, showing higher frequencies of specific arousal indicating behaviour with increasing RIs (cf. Table 5). F4 was highly and specifically aroused when subordinated to F2 and F12 with less agonistic display, showing higher frequencies of "Bury" with decreasing RIs. There are two possible explanations for the absences of agonistic efforts in F1 and F3 to maintain superiority (cf. Table 4) and for changes in their superiority without corresponding changes in levels and states of arousal

(cf. Table 5): a) The attachment of F3 to F1 and the established pair-bond between F1 and M1 implied so much security in these females that changes in superiority were not of central importance to them; or b) No changes in dominance occurred; retreating in these females does not imply subordination, but their social attachments secure them in such a way that an agonistic effort is not always necessary to demonstrate their dominance.

The maternal state activated by F2 as soon as young were present also provides a source of security, but not to such an extent as the long-lasting attachments for F3 and especially for F1. Although maternal behaviour was of high intensity, including "defence" of the young, it still was adequate and functional. F2 showed more "Anal-licking", contact behaviour and especially "Nibble" towards her own than other young. The persistent orientation towards young and, when present, the perception of other young may "switch on" motivations (and possibly physiological processes) related to the maternal state leading to an incomplete form of a mother-young-attachment. Salzen (1978) discusses that "impoverished or stunted attachments will give exaggerated orientation behaviours". Such mechanisms are supposed to be relevant for F2 in relation to other young.

A specific activation of aggressive motivation occurred in females F4, F12 and F31. This activation showed less with respect to amounts of agonistic behaviour, but more in a persistent orientation towards keeping other females at distance. Especially in F4 this specific activation is assumed to correspond to her lack of social and spatial attachments. Henry and Stephens (1977) report that mice, not able to form territorial and social attachments, engage in a chronic struggle for dominance, accompanied by high arousal, which can lead to pathologic changes in organs and physiological reactions. For F4, which came into this group as a nearly adult female, it can be supposed that her spatial orientation as well as her familiarity with the other females, even after several years living in the enclosure, is still different from those of the other females born in this enclosure. It remains to be investigated whether and how the mechanisms described can be related to specific behavioural and motivational components of the species' natural equipment for a pair-bond. It seems possible, however, that specific components were overactivated to compensate short-comings of the non-pair-bonded females to such an extent that stress could be held low or moderate and regular reproduction remained possible.

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Zusammenfassung

Soziale Beziehungen und individuelle Bewältigungsreaktionen in einer Gehegegruppe mittelamerikanischer Agutis (Dasyprocta punctata)

Es wurde eine Gehegegruppe mittelamerikanischer Agutis, bestehend aus 20 Tieren, beobachtet. Die individuellen Situationen und Reaktionen der Weibchen in der Gruppe sollten erfaßt werden. Es bestand eine Paarbindung zwischen dem adulten Männchen und dem ältesten Weibchen F1 sowie eine gegenseitige Bindung zwischen F1 und ihrer adulten Tochter F3. Eine weitere adulte Tochter (F2) zeigte übertriebenes mütterliches Verhalten sowohl gegenüber den eigenen als auch gegenüber den Jungtieren der anderen Weibchen. F2 und deren subadulte Tochter sowie eine subadulte Tochter von F1 und ein nicht in der Gruppe geborenes adultes Weibchen zeigten keine dauerhafte soziale Bindung. Für diese vier Weibchen korrelierten die Häufigkeiten von einigen agonistischen Verhaltensweisen und von Erregungsindikatoren mit ihren Ausweichhäufigkeiten gegenüber bestimmten Weibchen. Dieses weist auf eine spezifische Aktivierung aggressiver Motivation, begleitet von spezifischen Erregungszuständen, hin. Es wird die Hypothese aufgestellt, daß sich in der Aktivierung und teilweisen Überaktivierung spezifischer Motivationen und Verhaltensbereiche diese individuellen Reaktionen entwickelten, über die die spezifischen sozialen Situationen der Weibchen zu bewältigen waren. Diese Mechanismen ermöglichten eine Gruppensituation, in der die Belastungen der Tiere mäßig blieben und eine regelmäßige Reproduktion möglich war.

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The contribution of cranial indeterminate growth to non-geographic variation in adult *Proechimys albispinus* (Is. Geoffroy) (Rodentia: Echimyidae)

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Abstract

Analysed the contribution of cranial indeterminate growth in 19 metric characters to intrapopulation variation in *Proechimys albispinus* (Is. Geoffroy). Individuals were assigned to eight age classes on the basis of tooth eruption and surface wear criteria. The variation in skull characters was partitioned into age and residual components in adult individuals of age classes 6–8. An average of 17.34 percent of the variation in skull traits is due to the age effect in the three combined age classes of adults, and the remaining 82.66 percent accounts for residual variation within age classes. Discriminant function analysis correctly classified 80 percent and 72 percent of individuals to age classes 6 and 7, respectively, whereas all individuals in age class 8 were correctly classified. The implications of these findings for the taxonomy and systematics of the genus *Proechimys* are discussed.

Introduction

The genus *Proechimys* comprises a large number of species and is taxonomically complex and poorly understood. The difficulty to identify taxonomic units in *Proechimys* has been attributed to unusual levels of intrapopulational variation in morphologic characters traditionally used in mammalian systematics (Thomas 1928). Recently, Patton and Rogers (1983) demonstrated the increase in cranial dimensions in adult individuals to be the main source of intrapopulational variation in *P. brevicauda*, since sexual size dimorphism is minimal in this species. The results of Patton and Rogers (1983) are valid for *P. brevicauda* and their generality remains to be determined. The objective of this paper is to assess the contribution of cranial indeterminate growth to intrapopulational variation in *P. albispinus* (Is. Geoffroy), as a step toward the understanding of patterns of non-geographic variation in *Proechimys* and their implications for the taxonomy of the genus.

Materials and methods

A total of 106 specimens of *P. albispinus* collected in the vicinity of Fazenda Pedra Redonda, Jequié (13°15′ S, 40°05′ W), state of Bahia, northeastern Brazil during 1952 and 1953, available in the mammal collection of the Museu Nacional (Rio de Janeiro) was examined in this study. Age categories were defined on the basis of tooth eruption and surface wear criteria as follows (Fig. 1):

Age 6: P4, M1, and M2 with internal fold not completely isolated, M3 worn but with internal fold not isolated;

Age 7: M1, M2, and M3 with internal fold completely isolated;

Age 8: P4 with internal and main fold completely isolated, M1 with internal fold completely worn, main fold completely isolated, M2 with internal fold completely isolated, main fold not completely isolated, M3 with internal fold completely formed and isolated, main fold not isolated.

Age classes 1, 2, 3, and 4 are juveniles and age class 5 represents adolescent individuals according to Moojen's (1948) general criteria for the genus *Proechimys*. Individuals from age classes 6–8 are adults

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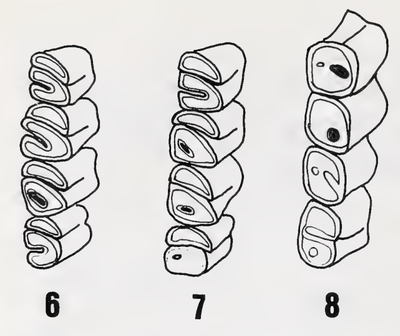


Fig. 1. Three late age classes for *Proechimys albispinus* (Is. Geoffroy) based on the pattern of surface wear of right maxillary toothrow (see text for description of age classes)

(Moojen 1948) and were selected for the analysis of the contribution of cranial indeterminate growth to within-population variation.

Nineteen cranial dimensions defined by Patton and Rogers (1983) were recorded for 63 adult individuals [age classes 6 (N = 26), 7 (N = 19), and 8 (N = 18)], as follows (Fig. 2): greatest length of skull (GSL); zygomatic breadth (ZB); palatal length B (PLB); mastoid breadth (MB); rostral breadth (RB); basilar length of Hensel (BaL); cranial depth (CD); rostral depth (RD); alveolar length of upper tooth row (MTRL); least nasal length (NL); least interorbital constriction (IOC); rostral length (RL); maxillary breadth (MaxB); diastema length (D); length of incisive foramen (IFL); length of tympanic portion of auditory bulla (BuL); post-palatal cranial length (PPL); and width of the mesopterygoid fossa (MFW).

Descriptive statistics including means and standard deviations were calculated for the 19 cranial traits for individuals in age classs 6–8. A preliminary analysis of variance indicated that only rostral length in age classs 7 and upper tooth row length in age class 8 differ significantly between the two sexes. Sexual size dimorphism is therefore virtually non-existent in *P. albispinus*, and sexes were pooled for the analysis of the added component of age variation due to indeterminate growth.

Table 1. **Statistics of variation for 19 cranial characters in the three age classes of adults of *Proechimys albispinus* (Is. Geoffroy)**

See text for explanation of character abbreviations

Age classes	6		7		8				
Characters	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	P	AVC	WVC
GSL	45.13	(1.13)	46.78	(1.36)	47.69	(0.57)	0.0001	42.99	57.01
ZB	34.02	(1.05)	35.46	(1.26)	36.41	(0.89)	0.0001	39.42	60.58
PLA	15.92	(0.72)	16.83	(0.81)	17.24	(0.57)	0.0001	31.59	68.41
PLB	7.33	(0.46)	7.67	(0.59)	7.95	(0.19)	0.0052	13.37	86.63
MTRL	7.63	(0.23)	7.68	(0.46)	7.59	(0.29)	0.6547	0.00	100.00
D	11.00	(0.61)	11.75	(0.65)	11.99	(0.50)	0.0001	30.35	69.65
RL	18.32	(0.93)	19.11	(0.88)	19.87	(0.77)	0.0001	33.58	66.42
NL	15.29	(0.85)	15.94	(0.97)	15.98	(0.51)	0.0118	10.71	89.29
IOC	10.71	(0.83)	10.86	(0.45)	11.65	(0.70)	0.0040	18.84	81.16
RB	6.61	(0.73)	6.48	(0.29)	6.54	(0.43)	0.8933	0.00	100.00
CD	12.45	(0.40)	12.45	(0.41)	12.85	(0.35)	0.0134	13.27	86.73
RD	8.70	(0.47)	9.02	(0.42)	9.44	(0.31)	0.0001	32.03	67.97
MaxB	7.92	(0.55)	8.35	(0.45)	8.40	(0.23)	0.0016	14.79	85.21
ZB	23.80	(0.82)	24.45	(0.58)	24.65	(0.54)	0.0009	16.86	83.14
BuL	9.95	(0.63)	10.10	(0.50)	10.18	(0.59)	0.4709	0.00	100.00
PPL	21.61	(0.72)	22.07	(0.77)	22.23	(0.59)	0.0171	8.43	91.57
IFL	3.99	(0.40)	4.25	(0.82)	4.00	(0.58)	0.1945	0.00	100.00
MFW	3.71	(0.87)	4.51	(1.06)	5.22	(0.82)	0.0003	23.25	76.75
MB	18.66	(0.69)	19.10	(0.55)	19.12	(0.57)	0.3224	0.00	100.00
Mean variance component								14.34	82.66

Statistics given are mean ($\bar{x}$), standard deviation (SD), significance level of an analysis of variance (P), and variance components associated with among-(AVC) and within-age classes (WVC) as sources of variation.

Significant differences among the age classes were tested for each character with a univariate analysis of variance (ANOVA). The factor age class was treated as a random variable (WINER 1971), and variation in cranial characters was further partitioned into within- and among-classes components of variance. Variance components can be estimated by different methods including the least squares procedure (SOKAL and ROHLF 1981). In the present study we used maximum likelihood estimates because of their statistical properties (SEARLE 1971; LINDGREN 1976; VAN VLECK and SEARLE 1979).

The degree of distinctiveness of each of the three adult classes was further assessed by discriminant function analysis (MORRISON 1976). The factor age class was treated as a single classification variable and posterior probabilities of correct allocation to the predicted groups were calculated. The posterior probabilities of correct classification were expressed as percentages. All statistical analyses were performed with SAS-PC version 6.03 (SAS Institute 1988).

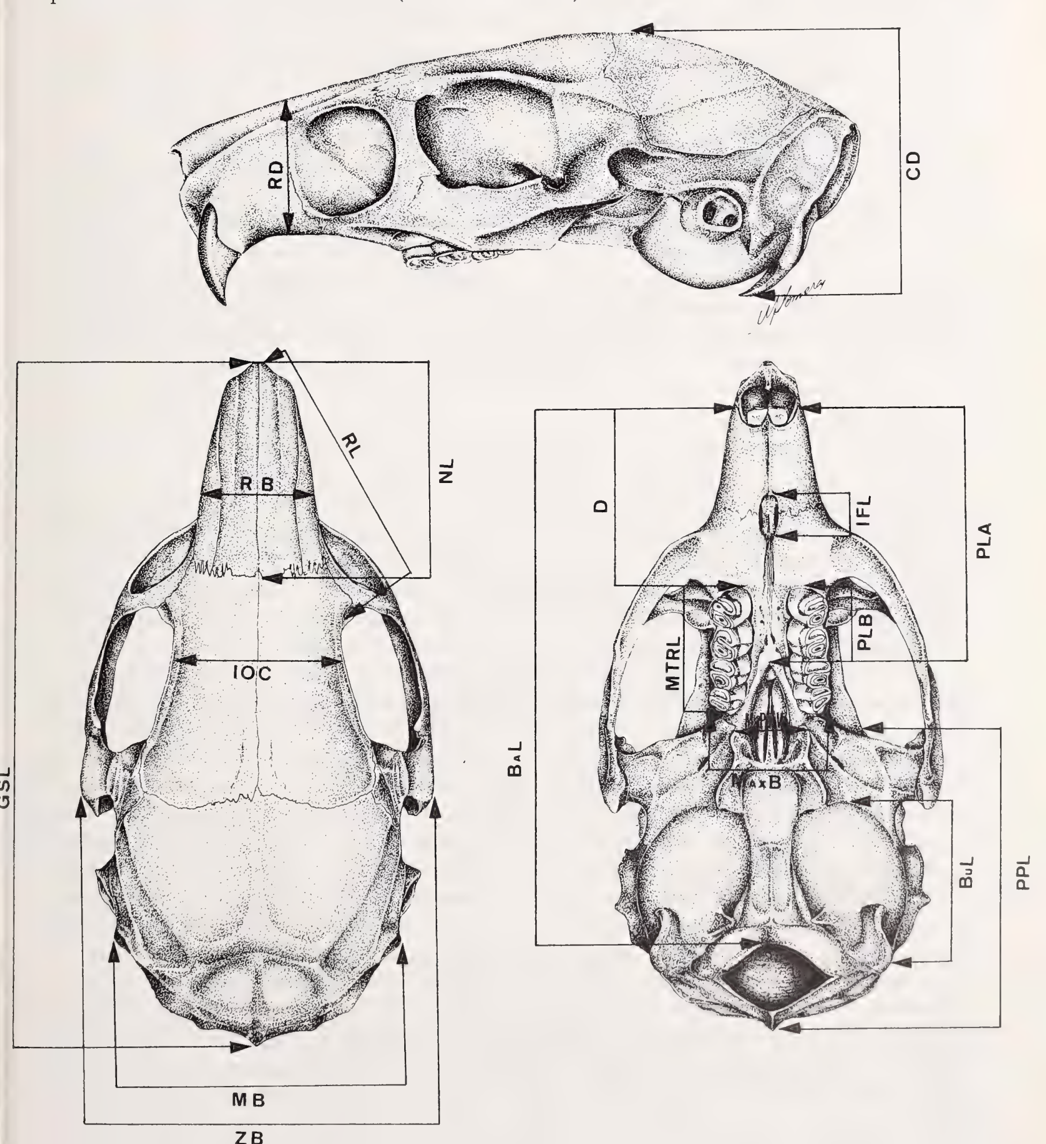


Fig. 2. Nineteen measurements taken from the skulls of *Proechimys albispinus* (Is. Geoffroy), (see text for explanation of measurement abbreviations)

Results

Most character means increase in the three age classes as expected, reflecting the fact that individuals continue to grow after they have become adults (Table 1). Univariate ANOVAs showed that all characters except mastoid breadth, length of upper tooth row, diastema, bulla length, and width of the mesopterygoid fossa differ significantly among age classes (Table 1).

An average of 17.34 percent (range, 0.00–42.99 percent) of the variation in cranial traits can be assigned to an increase in cranial dimensions due to indeterminate growth in adult individuals (Table 1). In about a third of the characters more than 30 percent of the variation in cranial dimensions can be accounted for by indeterminate growth in the adult age classes. The remaining 82.66 percent (range, 53.72–100 percent) of the variation is due to residual variability within age classes (Table 1). Discriminant functions correctly allocated 80 and 72 percent of the individuals in age classes 6 and 7 to their predicted groups, whereas all individuals of age class 8 were correctly classified to their age group (Table 2).

Table 2. **Posterior probability of correct allocation of adult individuals of *Proechimys albispinus* (Is. Geoffroy) of age classes 6–8 to their predicted age classes**

Probabilities of correct classification are expressed as percentage

Predicted age classes		6	7	8
Actual age classes	6	80.00	16.67	3.33
	7	16.00	72.00	12.00
	8	0.00	0.00	100.00

Discussion

The analysis of geographic patterns of variation is an important step for the understanding of mechanisms involved in the process of differentiation within a species (Patton and Smith 1989). It is nevertheless important to assess properly the magnitude of within-population variability before evaluating the extent of geographic variation (Thorpe 1983). Variation within populations can usually be ascribed to ontogenetic, sexual, random, and environmental factors (Straney 1978; Chesser 1983; Schmidly et al. 1988).

Variation in skull characters in *Proechimys* seems to be mostly due to indeterminate growth in adult individuals, since sexual size dimorphism is apparently very low in this genus (Martin 1970; Straney 1978; Patton and Rogers 1983; this study). The mean value of 17.34 percent found for variation in cranial dimensions in *P. albispinus* due to the age effect of combined age classes 6–8, is smaller than the value of 27.76 percent obtained by Patton and Rogers (1983) for *P. brevicauda*. We believe the amount of cranial variation due to age in the two species can be compared, since our combined age class 6–8 is roughly similar to age classes 8–10 used by Patton and Rogers (1983). It should be noted, however, that age classes based on tooth wear criteria may not be strictly a function of time (= chronological age), but may reflect differences in diet, soil type, habitat, and health. These factors alone or in combination could conceivably account for differences in the variance of cranial traits assignable to age classes in different populations or species. *P. albispinus* also differs from *P. brevicauda* in the amount of variation in skull traits that can be attributed to the age effect. Comparison of our data with those for *P. brevicauda* (Table 3 of Patton and Rogers 1983) shows that, for example, the component of variance due to age in greatest skull length is 28.4 percent in *P. brevicauda* and 42.99 percent in *P. albispinus*. The lack of correspondence in the direction of variation in cranial traits due to age is confirmed by non-significant correlations between estimates of variance components due to age for *P. albispinus* and *P. brevicauda* (Kendall's $\tau = -0.054$; Spearman's $r = -0.101$: $P > 0.05$).

Our results thus indicate that variation in skull traits due to age effects in *P. albispinus* is not as pronounced as in *P. brevicauda*, and the characters showing the largest amount of variation due to age are not the same in the two species. Nevertheless, despite the fact that most variation in cranial traits in *P. albispinus* is residual (average of 82.66 percent), the potential of age variation to confound the analysis of geographic variation and taxonomic studies at the species level does exist, and is demonstrated by the moderate to high percentages of correct allocation to age categories provided by the discriminant function analysis. By way of example, it can be supposed that in a study of geographic variation one uses a sample of individuals of age class 6 from one locality, and a sample of individuals of age class 8 individuals from another locality. Regardless of the existence of cranial differences due to locality effects, the two populations would be almost completely discriminated solely because of variation in cranial dimensions due to age differences in the two samples.

The results of Patton and Rogers (1983) plus the findings of our study seem to indicate that relatively high levels of intrapopulational variation in skull dimensions due to indeterminate growth may be characteristic to the genus *Proechimys*. The substantial age component of variation in skull traits in adult individuals of *P. brevicauda* led Patton (Patton and Rogers 1984; Patton 1987) to suggest that many characters routinely used in small mammal systematics, as well as the multivariate morphometric methods usually employed, may be of questionable value in the study of the taxonomy and systematics of the genus *Proechimys*. Patton and Rogers (1983) further suggested that equivalent age classes should be used in studies of geographic variation.

The cautionary approach of Patton and Rogers (1983) is well taken, since the existence of high levels of intrapopulational variation may pose a serious problem whenever variation in geographic space is to be assessed (Thorpe 1983). It is possible that the standard morphometric traits and multivariate procedures can be of use if the intrapopulational component of variation can be properly quantified and statistically removed. To this end, the statistical procedure of size-independent canonical discriminant analysis (Strauss 1985) may be the appropriate tool to partition out the effect of age in metric dimensions in studies of geographic variation and specific differences in *Proechimys*, in spite of the existence of high levels of intrapopulational variation. Size-independent canonical discriminant analysis basically consists of removing the effect of within-group size variation by regressing each character separately on the first pooled within-group principal component (a multivariate estimate of size), and then employing canonical discriminant analysis with the residuals obtained from the regressions to analyse variation among populations (Strauss 1985).

The technique of size-independent canonical discriminant analysis has been applied with success to studies of geographic variation in *P. dimidiatus* (Pessôa and Reis 1990; Reis et al. 1990) and *P. iheringi* (Pessôa and Reis 1991), where relatively complex patterns of differentiation have been identified. We believe that the application of this procedure will prove very helpful in the study of the taxonomy and systematics of the genus *Proechimys*.

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Zusammenfassung

Der Anteil des unbegrenzten Schädelwachstums an der Variabilität von Schädeln gleicher Herkunft bei adulten Proechimys albispinus (Is. Geoffroy) (Rodentia: Echimyidae)

Igelratten (*Proechimys albispinus*) wachsen zeitlebens. In der vorliegenden Arbeit wird versucht, den Anteil der durch unterschiedliches Alter bedingten Variabilität an der Gesamtvariabilität bei adulten Tieren einer Population abzuschätzen. Dazu wurden die Tiere jeweils einer von acht Stufen des Gebißzustandes zugeordnet, die mit dem Alter korreliert sind. Der Einfluß des Alters auf 19 Schädelmaße wurde für die ältesten Klassen 6–8 geprüft. Er betrug etwa 17 % der Gesamtvariabilität innerhalb dieser Gruppe. Mit Hilfe einer Diskriminanzanalyse konnten 80 % der Tiere der Klasse 6, 72 % der Klasse 7 und 100 % der Klasse 8 richtig zugeordnet werden. Die Folgerungen für die Taxonomie werden diskutiert.

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Quantitative investigation of the area and volume in different compartments of the intestine of 18 mammalian species

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Abstract

Investigated the morphometric parameters of the small and large intestines of 18 mammalian species. A new method is described for morphometric study of intestines by means of planimetry using the entire intestine to calculate basal surface areas. In addition a computer-aided programme is presented for assessing surface enlargement of the intestinal mucosa at the light-microscopical level. The latter gives a surface enlargement factor which can be multiplied by the values gained from planimetry to give a final total surface enlargement of the intestine. The data are presented in coordinate systems and are used for calculating linear regression. The results show clearly that basal areas of small intestine, colon and total intestine scale almost isometrically to metabolic body weight, whilst caecum scales slightly negative allometrically. Areas of all intestinal compartments scale negative allometrically to absolute body weight. Volume shows positive allometric scaling to metabolic body weight and approximately isometry to absolute body weight (except for caecum: negative allometry).

The relation of area to volume in the form of ratios (area/volume) gives an estimate of the area available per unit volume. In this case smaller animals appear to have a more advantageous relationship of area to volume than large animals. This fact is interpreted as a correlate to the higher metabolic needs of smaller animals.

Introduction

It has long been recognized that size imparts profound consequences on structure and function in organisms and that food and size are interrelated (Schmidt-Nielsen 1975). The concept of scaling is concerned with the effects and consequences of changes in size. Isometry describes the situation where a change in any one linear dimension is accompanied by a change in all other linear dimensions in exactly the same proportion. Non-isometric scaling is termed allometry.

According to Kleiber's law (Kleiber 1961) basal metabolic rates scale to body mass in mammals with an exponent value of 0.75. It can be expected then that organs concerned directly with metabolic turnover also scale to body mass in accordance with this factor. Most obviously the acquisition and utilization of nutrition and the organ system involved in these processes (gastrointestinal tract) would fall into the category of these expectations. The development of homoiothermy and consequent high metabolic rates in mammals have been reviewed by Karasov and Diamond (1985) (see also Duncker 1989).

Certain generalities are obvious with respect to the appearance of the gut in extreme dietary forms, such that voluminous large intestines (caecum and/or colon) are most commonly found in herbivores (Grassé 1973; Parra 1978; Langer 1986, 1987a, b; Stevens 1988), whilst a shorter and more simply constructed large intestine is rather characteristic of faunivores (Chivers and Hladik 1980, 1984; Karasov and Diamond 1988). The occurrence as well as relative size of caecum and colon has been correlated to dietary adaptations (Ulyatt et al. 1975; Janis 1976; Hladik 1978; Hume and Warner 1980; Björnhag 1987; Langer 1987b; Chivers 1989; McBee 1989). In some species a caecum is missing altogether (Mitchell 1905; Gorgas 1967; Arvy 1972; Behmann

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1973). The large group of animals which use a dietary adaptation intermediate between strict herbivory and faunivory are much less typical or uniform in their morphological characteristics. Moreover, a pliancy in the form of the intestinal tract and an adaptative ability to various ambient conditions makes a strict categorization difficult (Langer 1984; Green and Millar 1987; Karaso and Diamond 1988; Hofmann 1989). Despite these constraints a number of authors has attempted to develop a rough scheme for grouping animals based on various criteria (Chivers and Hladik 1980, 1984; Martin et al. 1985; Chivers 1989; see also Langer 1987b; Snipes 1991). Only the above-cited investigators, however, have used morphometry to quantify these criteria.

Although many of the characteristics of gut structure in a particular species may be so obvious as to lead one to the supposition that it belongs to a particular dietary group, the use of quantitative data can either support or negate these subjective inferences.

Thus, in the present study parameters of area and volume of the small and large intestines of 18 mammalian species were measured by use of modern morphometric techniques and the data subjected to allometric analysis.

Materials and methods

18 different mammalian species (three animals per species with either one female and two males or two females and one male) were used in the present study. They were chosen according to two main criteria. One criterion used was to choose taxonomically closely related species (in order to keep the taxonomic influences at a low level), who differed substantially in body weight. Another criterion was to choose different species employing various dietary adaptations (e.g., faunivory, herbivory and intermediate forms as well as rumination). An attempt was made to handle all animals as similarly as possible in order to reduce the influence of this factor on the quantitative results. Due to the difference in availability of some animals from such sources as diverse as the laboratory or abattoir or the field this was not always possible. Table 1 is a listing of all animal species used in the present study.

In most cases fixation of the intestine was performed according to Fenwick and Kruckenberg (1987) via intraluminal filling. In small mammals segments of the gut used for light microscopy were very gently injected with Lillie's buffered formol avoiding distension of the lumen. The gut (duodenum to rectum) was opened lengthwise. From selected areas (see Fig. 1) 0.8 mm diameter

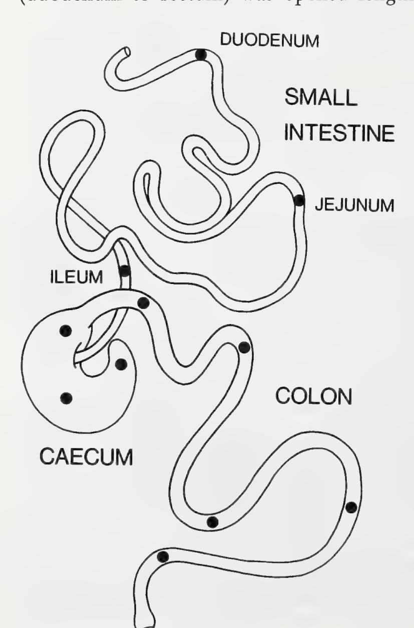


Fig. 1. Sampling for imagine analysis. Schematic drawing of the small and large intestines including caecum of an idealised intestine of a mammal. Black circles indicate sites of sampling. Diameters of 0.8 mm were punched out after the intestine had been opened lengthwise. For small intestine the sample for duodenum was taken within the first few cm of the start of the small intestine; ileum was taken a few cm orad to the ileocaecal junction. Jejunum was selected as being equidistant between these two points. The caecum was sampled in three areas: apex, corpus and near the caecocolical junction. The colon was divided into five equidistant segments from caecocolical junction to rectum. Within each of these segments a sample was taken

samples were punched out with a cork borer and placed immediately in Bouin's fluid and processed according to conventional methods for paraffin histology. Directly after sampling, appropriate lengths were sequentially flattened gently between two glass plates. The contours of the flattened gut were outlined immediately onto transparent paper and then areas of the contours were measured by means of a planimeter (in mm^2) (MOP, Kontron, Munich, FRG). The sum of these measured outlines for caecum and colon are termed BASAL AREAS.

By use of this method the disadvantages of sampling and extrapolation from measured samples to total lengths were avoided. Only in the case of the small intestine a 10-cm long segment (and not the entire small intestine) was excised and opened lengthwise. It was then flattened between the glass plates and subsequently the contours outlined. From this measured segment the entire area of the small intestine in mm^2 was calculated by multiplying this value times the total length of small intestine (Pénzes and Skála 1977).

The values of basal areas represent the means of three individual measurements of each outlined contour. A final mean was then calculated from the measurements gained from the three individuals of each species, which was then used for further statistical analysis. The various regions within the caecum or colon as depicted in Fig. 1 were not analysed separately in the present study, but rather were pooled to give one mean value for a species for caecum, for colon and for small intestine.

To access the increase in surface areas over and beyond this basal area, i.e., due to microscopically visible villi, crypts, mounds, plicae etc., the samples taken for light microscopy as described above and illustrated in Fig. 1 were subjected to analysis using a newly designed imagine analysing programme (IBAS, Kontron). The device consisted of a host computer and an image processing cabinet. The host computer controlled the system, assisted both interactive and automatic image analysis and performed the basic treatment of the data measured. A TV camera (VIDICON, Bosch, Stuttgart, FRG), mounted on a light microscope (UNIVERSAL, Zeiss, Oberkochen, FRG) was interfaced to the image-processing cabinet of the system. Images of the tissues were obtained using a 16× magnifying lens, stored in video memory after digitization and processed with a special processor included in the system.

The image analysing programme was developed to facilitate an automatic length measurement of both the flat tissue basal boundary and the corresponding folded surface boundary (i.e., the surface mucosal relief). Consequently, two values per individual field of view were measured. The programme included 1. image preprocessing to correct artifacts and to increase the overall contrast, 2. segmentation of the tissue from the background, and 3. identification and measurement of contour lengths. The programme was embedded into an easy-to-operate loop structure with interactive pauses for control and correction via mouse and digitizer tablet. After completion of a fixed number of measurements per specimen the scaled measurement values were stored permanently on harddisk. Accessing these values with a programme written in FORTRAN allowed to calculate a Surface Enlargement Factor (SEF) at the microscopical level by dividing the length of the folded surface boundary produced by the second-order (i.e. micro-anatomical) enlargements of the mucosa by the flat basal boundary (Fig. 2). This factor multiplied by the value obtained by planimetry (BASAL AREA) gives the final value of TOTAL AREA. Light-microscopical material from only 11 of the 18 species was available for determination of SEF values, as indicated in Table 1 with an asterisk.

Before routine measurement with this programme a pilot experiment was performed to standarize the number of sections (Zilles et al. 1982) and the number of measurements necessary for a statistically significant study according to the method of Baur (1969) which states that the sample size should never be less than twice the relative standard deviation of the samples, expressed as percentage. Volumes were calculated from measured parameters of length and basal areas according to the formula: $V = (\text{Basal area})^2 / 4 \times l$. All data were subjected to statistical analysis, primarily using linear regression curves with the help of Statgraphic and Harvard Graphics computer programmes. The values of the coefficients of correlation gave significance at the 0.1 % level.

Results

Table 1 is a compilation of the morphometric values gained in this study. Basal areas (measured by planimetry of flattened segments of gut) for each species are given in cm^2. Percentages of these values to the values for total intestine are also given. Surface enlargement factor (SEF) indicates the values measured by imagine analysis of histological sections. This factor multiplied by the basal area gives total areas which are also presented in Table 1 as cm^2 and percentages. Volumes are presented as ml and percentage of total intestinal volume. In the following account the term "total intestine" means additive values from small intestine, caecum and colon. Whenever the term "large intestine" appears both caecum and colon are considered together.

Table 1. **Empiricle values of the parameters of area and volume for small and large intestines of the 18 mammalian species used in the present study**

Basal areas were measured by planimetry and are given in cm^2 (below each value is the percent for this intestinal compartment to the total intestinal value). SEF is the surface enlargement factor gained by imagine analysis on histological sections. Total areas are products of basal area × SEF and are given in cm^2 and in percentages. Volumes are calculated values and are presented in ml and percentage of total volume of small and large intestine together

Species	Basal area (cm^2)				SEF			Total area (cm^2)				Volume (ml)			
	Small int	Caecum	Colon	Total	Small int	Caecum	Colon	Small int	Caecum	Colon	Total	Small int	Caecum	Colon	Total
Vole[a] *Microtus agrestis* Body Wt 33.6 g	15.7 51.2 %	6.9 22.6 %	8.0 26.2 %	30.6	3.95	1.77	1.96	61.9 68.8 %	12.3 13.7 %	15.7 17.5 %	89.9	1.2 50.5 %	0.8 32.4 %	0.4 17.3 %	2.4
Dwarf hamster[a] *Phodopus sungorus* Body Wt 36.1 g	26.3 56.2 %	7.9 16.9 %	12.6 26.9 %	46.8	2.65	1.55	1.30	69.9 70.9 %	12.3 12.5 %	16.5 16.7 %	98.7	2.4 52.4 %	1.3 27.1 %	0.9 20.5 %	4.6
Mouse[a] *Mus musculus* Body Wt 47.5 g	46.1 68.0 %	8.6 12.6 %	13.1 19.3 %	67.8	2.56	1.81	1.57	118.3 76.6 %	15.5 10.1 %	20.6 13.4 %	154.4	4.6 58.3 %	1.7 21.5 %	1.6 20.2 %	7.9
Gerbil[a] *Meriones unguiculatus* Body Wt 81.3 g	34.3 59.3 %	11.3 19.5 %	12.3 21.3 %	57.9	2.55	1.75	1.66	87.7 68.5 %	19.7 15.4 %	20.6 16.1 %	128.0	3.6 50.1 %	2.7 37.1 %	0.9 12.7 %	7.2
Mole rat *Spalax ehrenbergi* Body Wt 122.5 g	30.6 40.4 %	30.8 40.7 %	14.3 18.9 %	75.7	–	1.55	1.50	–	47.7	29.8		2.9 41.4 %	3.2 45.7 %	0.9 12.9 %	7.0
Golden hamster[a] *Mesocricetus auratus* Body Wt 155.8 g	75.4 47.4 %	35.3 22.2 %	48.3 30.5 %	159.0	3.86	1.68	1.30	291.9 70.3 %	59.7 14.4 %	63.5 15.3 %	415.1	11.5 44.5 %	8.9 34.6 %	5.4 20.9 %	25.8
Rat[a] *Rattus norvegicus* Body Wt 298.0 g	113.4 69.9 %	26.6 16.4 %	22.2 13.7 %	162.2	2.26	1.55	1.66	257.3 76.7 %	41.2 12.3 %	36.8 11.0 %	335.3	11.4 49.6 %	8.9 38.7 %	2.7 11.7 %	23.0
Muskrat[a] *Ondatra zibethicus* Body Wt 843.3 g	203.6 41.0 %	165.3 33.3 %	127.1 25.6 %	496.0	2.80	2.52	2.11	571.2 45.4 %	417.1 33.2 %	269.1 21.4	1257.4	44.0 26.7 %	98.2 59.5 %	22.6 13.7 %	164.8
Guinea pig[a] *Cavia aperea* Body Wt 979.4 g	298.9 44.9 %	174.1 26.1 %	193.4 29.0 %	666.4	3.21	2.24	1.56	961.4 58.1 %	391.0 23.6 %	303.0 18.3 %	1655.4	51.9 24.0 %	135.2 62.5 %	29.3 13.5 %	216.4

Rabbit[a]															
Oryctolagus cuniculus	442.2	512.5	268.1	1222.8	3.50	2.18	1.80	1548.1	1121.1	485.2	3154.4	79.3	514.2	50.1	643.6
Body Wt 357.9 g	36.2 %	41.9 %	21.9 %					49.1 %	35.5 %	15.4 %		12.3 %	79.9 %	7.8 %	
Nutria[a]															
Myocastor coypus	1040.1	362.1	312.7	1714.9	3.71	1.81	2.09	3865.7	655.9	654.5	5176.1	254.9	279.5	84.7	619.1
Body Wt 6316.7 g	60.7 %	21.1 %	18.2 %					74.7 %	12.7 %	12.6 %		41.2 %	45.2 %	13.7 %	
Dog															
Canis lupus	1124.8	57.7	251.6	1434.1	–	–	–	–	–	–	–	373.0	34.5	120.0	527.5
Body Wt 13,750 g	78.4 %	3.9 %	17.5 %									70.7 %	6.5 %	22.7 %	
Sheep															
Ovis ammon	6377.4	298.9	2433.6	9109.9	–	–	–	–	–	–	–	1503.2	284.4	766.5	2554.1
Body Wt 42,500 g	70.0 %	3.3 %	26.7 %									58.9 %	11.1 %	30.0 %	
Goat															
Capra aegagrus	3770.3	192.6	1341.2	5304.1	–	–	–	–	–	–	–	1187.0	140.6	340.9	1668.5
Body Wt 52,500 g	71.1 %	3.6 %	25.3 %									71.1 %	8.4 %	20.4 %	
Human[a]															
Homo sapiens	8044.8	145.6	710.5	8900.9	3.66	1.79	2.483	29512.4	261.7	1764.9	31539.0	14524.2	176.6	453.2	15154.0
Body Wt 86,660 g	90.4 %	1.6 %	8.0 %					93.6 %	0.8 %	5.6 %		95.8 %	1.2 %	3.0 %	
Pig															
Sus scrofa	10047.3	447.0	5405.3	15899.6	–	–	–	–	–	–	–	4406.6	564.8	3808.1	8779.5
Body Wt 111,850 g	63.0 %	3.0 %	34.0 %									50.2 %	6.4 %	43.4 %	
Cow															
Bos primigenius	27393.5	783.8	7426.9	35604.2	–	–	–	–	–	–	–	14662.8	857.7	4598.8	20119.3
Body Wt 474,300 g	76.9 %	2.2 %	20.9 %									72.9 %	4.3 %	22.9 %	
Horse															
Equus przewalskii	42183.4	9195.4	27928.1	79306.9	–	–	–	–	–	–	–	46897.3	56083.0	83892.7	186873.0
Body Wt 520,000 g	53.2 %	11.6 %	35.2 %									25.1 %	30.0 %	44.9 %	

[a] Material available from these species for both Basal areas and Total areas.

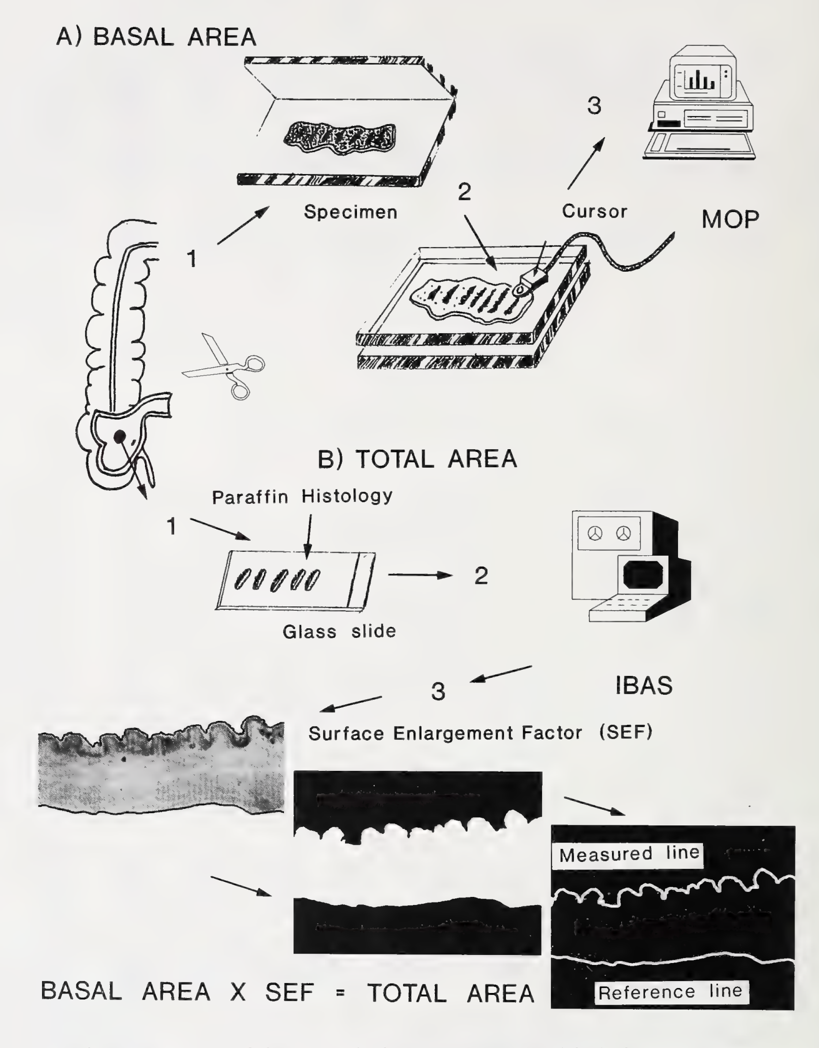


Fig. 2. Pictorial representation of the method of measurement (modified after Snipes 1991). A) Basal areas are obtained by opening the intestines lengthwise and taking appropriately long specimens (1) and flattening them between glass plates (2). A transparent paper is used to trace the outlines which are then measured with a cursor attached to the semi-automatic planimeter MOP (3). For Total areas (B) a 0.8 mm specimen is punched out of the intestine (1) (see Fig. 1 for sampling scheme) and processed for light microscopy. Sections (2) are analysed with the use of the IBAS imagine analysor to give a factor of surface enlargement (SEF) (3). The pictures at the bottom give three steps in the production of an image for measuring. At far right, the SEF value results from the measured line in relation to the reference line. Total area is the product of basal area and SEF

Areas

The calculated regression lines of the basal areas for all 18 species versus metabolic body weight are given in Fig. 3a–d. Small intestine (Fig. 3a), colon (Fig. 3c) and total intestine (Fig. 3d) scale close to isometry with respect to metabolic body weight. In all three cases the coefficients of correlation are significant at the 0.1 % level [small intestine: slope 1.01 (r = 0.99); colon: slope 0.95 (r = 0.94) and total intestine: slope 0.96 (r = 0.99)]. The data for caeca scale negative allometrically (slope 0.68; r = 0.89). Plotted against absolute body weight instead of metabolic body weight, the slopes for all intestinal regions fall to negative allometry (graphs not shown) (small intestine: slope 0.76; colon: slope 0.71; total intestine: slope 0.72 and caecum: slope 0.51). Correlation coefficients are all significant at the 0.1 % level.

Fig. 4a–d present the respective graphs for total areas (i.e. basal area × SEF) for the 11 species noted with an asterisk in Table 1. In these cases small intestine and total intestine scale isometrically with metabolic body weight (slopes 1.01 and 1.00, respectively); caecum and colon negative allometrically (slopes 0.77 and 0.89, respectively). Scaled to absolute body weight all values are much decreased (small intestine: slope 0.76; caecum: 0.57; colon: 0.66; and total intestine: 0.71).

Volumes

Calculated volumes for small intestine, colon and total intestine all scale positive allometrically with metabolic body weight (slopes, respectively, 1.33; 1.35; 1.30) (Fig. 5). Caecum is almost isometric (slope 1.03) (Fig. 5b). All "r" values are significant at the 0.1 % level. Plotted against absolute body weight these values do not decrease to negative allometry as was the case with areas, except for caecum, showing the most dramatic decrease (slopes: small intestine 0.99; caecum 0.77; colon 1.01; and total intestine 0.97) (graphs not shown).

Table 2. **Coefficient of gut differentiation**

Represents the ratio of the area of the large intestine divided by the area of the small intestine

	Basal area		Total area	
Human	11	(F)	7	(F)
Dog	27	(F)	–	
Cow	3	(R)	–	
Goat	41	(R)	–	
Sheep	43	(R)	–	
Rat	43	(I)	30	(I)
Mouse	47	(I)	31	(I)
Pig	58	(I)	–	
Nutria	65	(I)	34	(I)
Gerbil	68	(I–H)	46	(I)
Dwarf hamster	78	(H)	41	(I)
Horse	88	(H)	–	
Vole	95	(H)	45	(I)
Golden hamster	111	(H)	42	(I)
Guinea pig	123	(H)	72	(H)
Muskrat	144	(H)	120	(H)
Mole rat	147	(H)	–	
Rabbit	177	(H)	104	(H)

Large intestine = Caecum + Colon; all values × 100.

Rating: F = Faunivore: 0 – 30
I = Intermediate: 30 – 70
H = Herbivore: 70 +
R = Ruminant

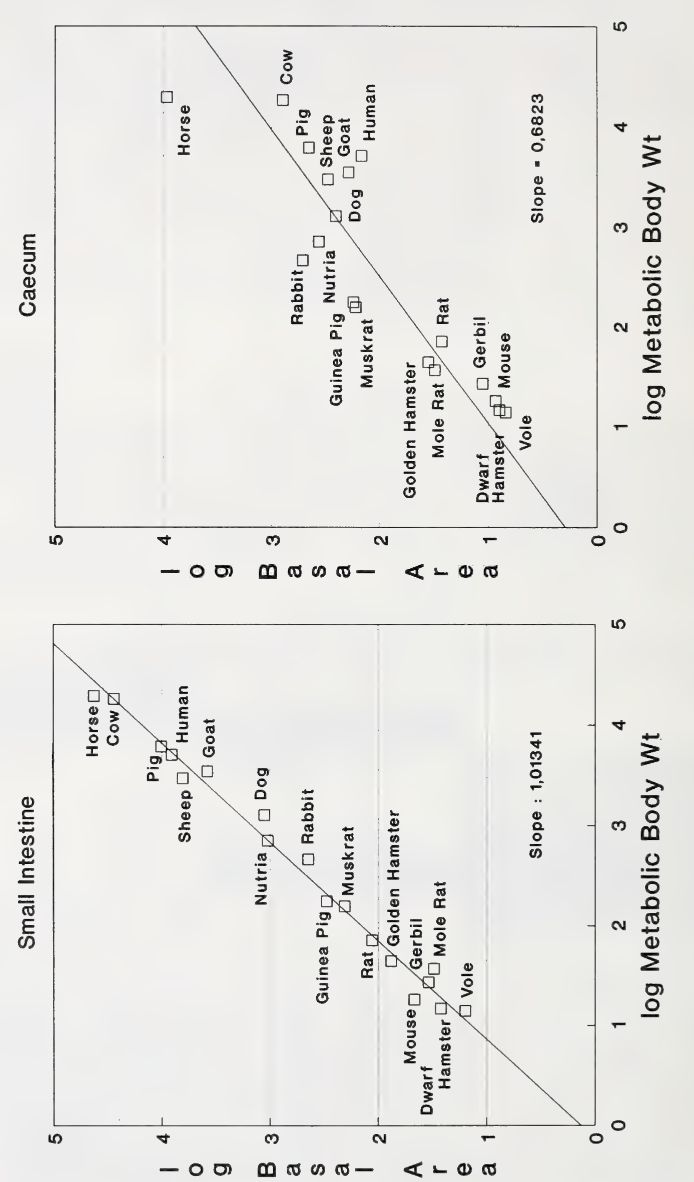

Small Intestine
Caecum
log Basal Area
log Metabolic Body Wt
Slope : 1,01341
Slope = 0,6823
Horse
Cow
Pig
Human
Goat
Sheep
Dog
Rabbit
Nutria
Muskrat
Guinea Pig
Golden Hamster
Rat
Gerbil
Mole Rat
Mouse
Vole
Dwarf Hamster
0 1 2 3 4 5

Fig. 3a

Fig. 3b

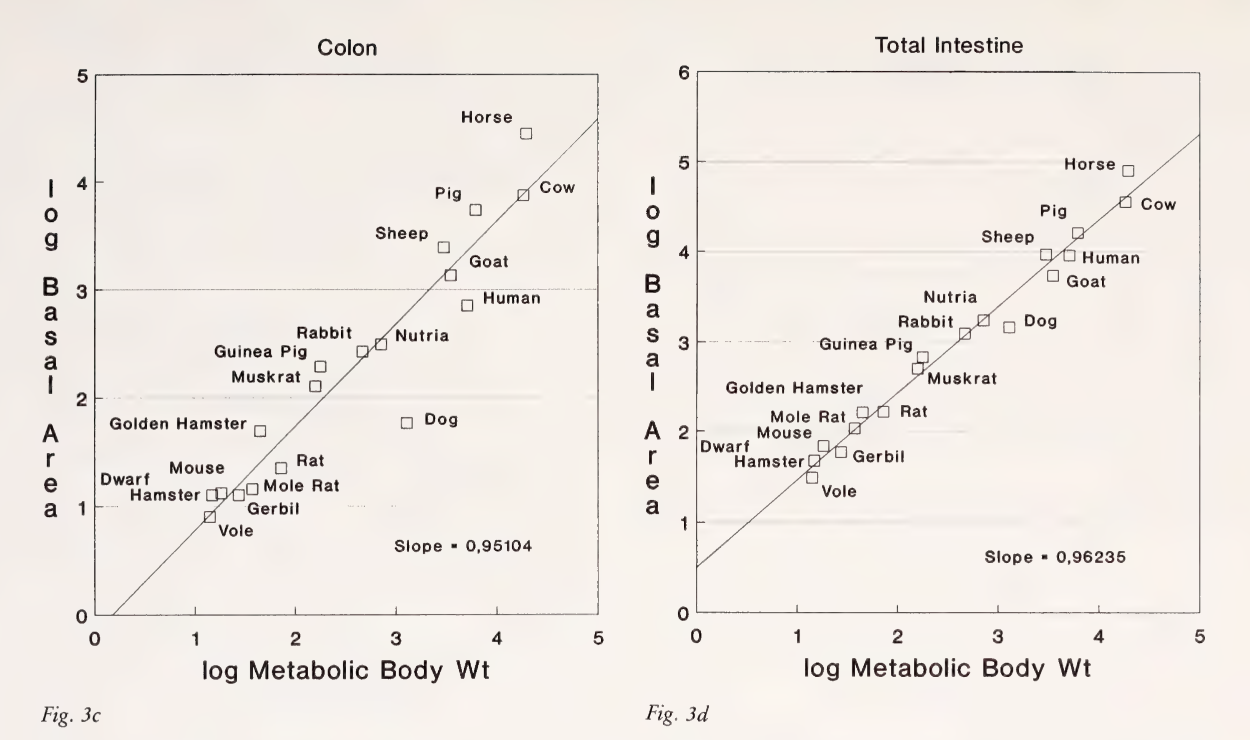


Fig. 3c

Fig. 3d

Fig. 3. Regression lines for basal areas (ordinate log cm^2) versus metabolic body weight (abscissa log grams). Slopes for the small intestine (3a), caecum (3b), colon (3c) and total intestine (3d) for the 18 animals were all significant by use of the coefficient of correlation at the 0.1 % level

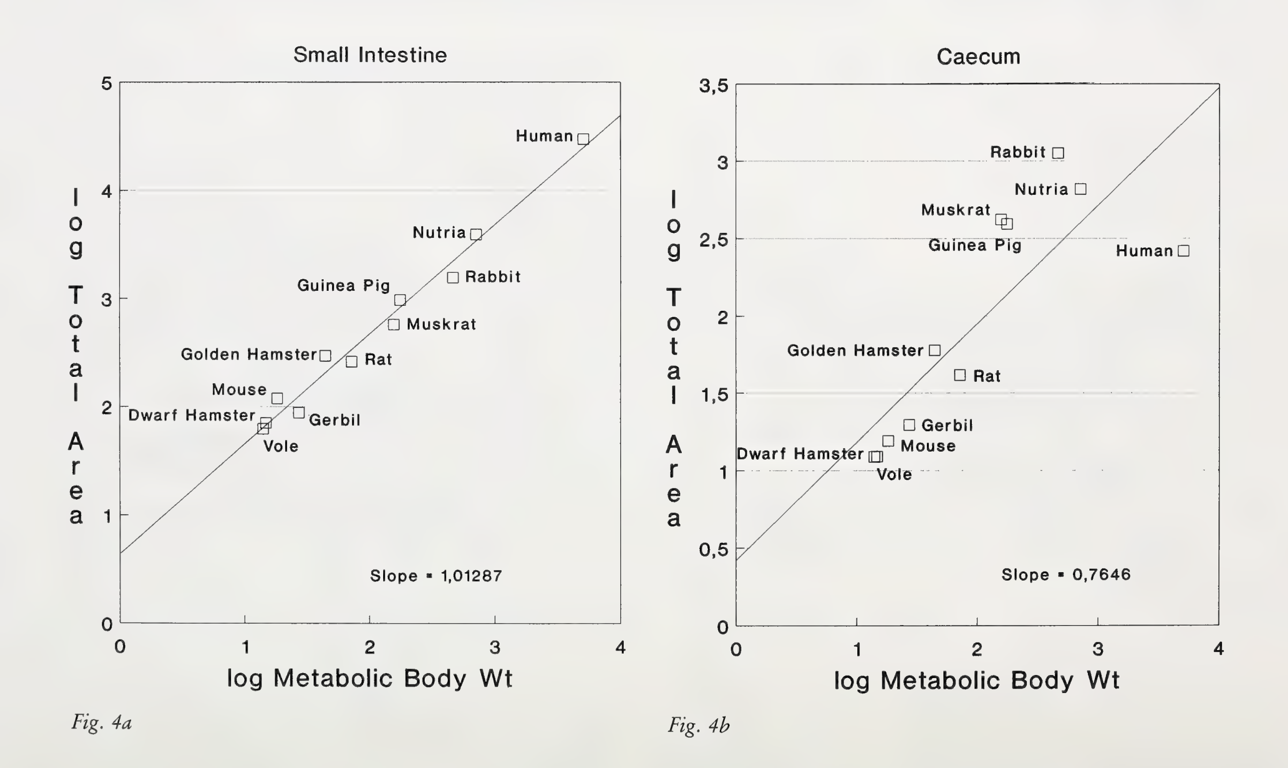

Small Intestine
log Total Area
log Metabolic Body Wt
Slope = 1,01287
Human
Nutria
Rabbit
Guinea Pig
Muskrat
Golden Hamster
Rat
Mouse
Dwarf Hamster
Gerbil
Vole
0
1
2
3
4
5
Caecum
log Total Area
log Metabolic Body Wt
Slope = 0,7646
Rabbit
Nutria
Muskrat
Guinea Pig
Human
Golden Hamster
Rat
Gerbil
Mouse
Dwarf Hamster
Vole
0
0,5
1
1,5
2
2,5
3
3,5

Fig. 4a

Fig. 4b

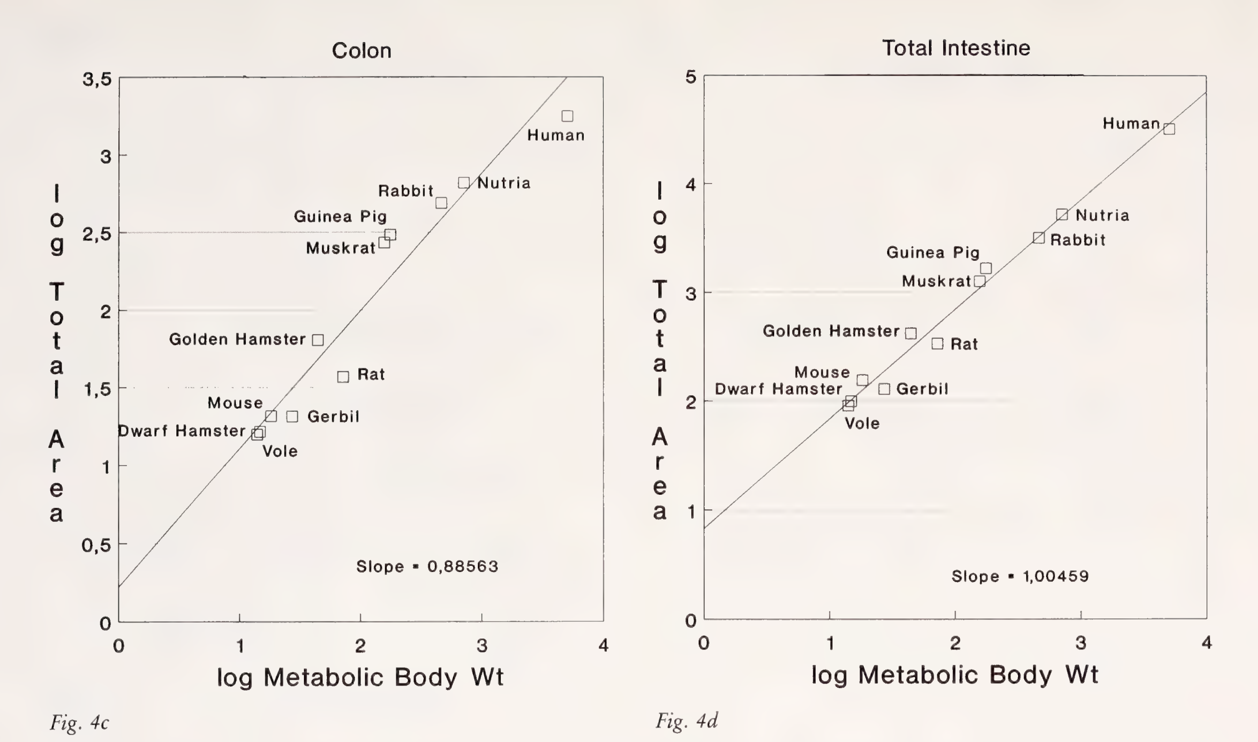


Fig. 4c

Fig. 4d

Fig. 4. Regression lines for total areas (basal area × SEF log cm^2) (ordinate) versus metabolic body weight (abscissa log grams). 4a: small intestine, 4b: caecum, 4c: colon, 4d: total intestine. The coefficients of correlation are significant at the 0.1 % level

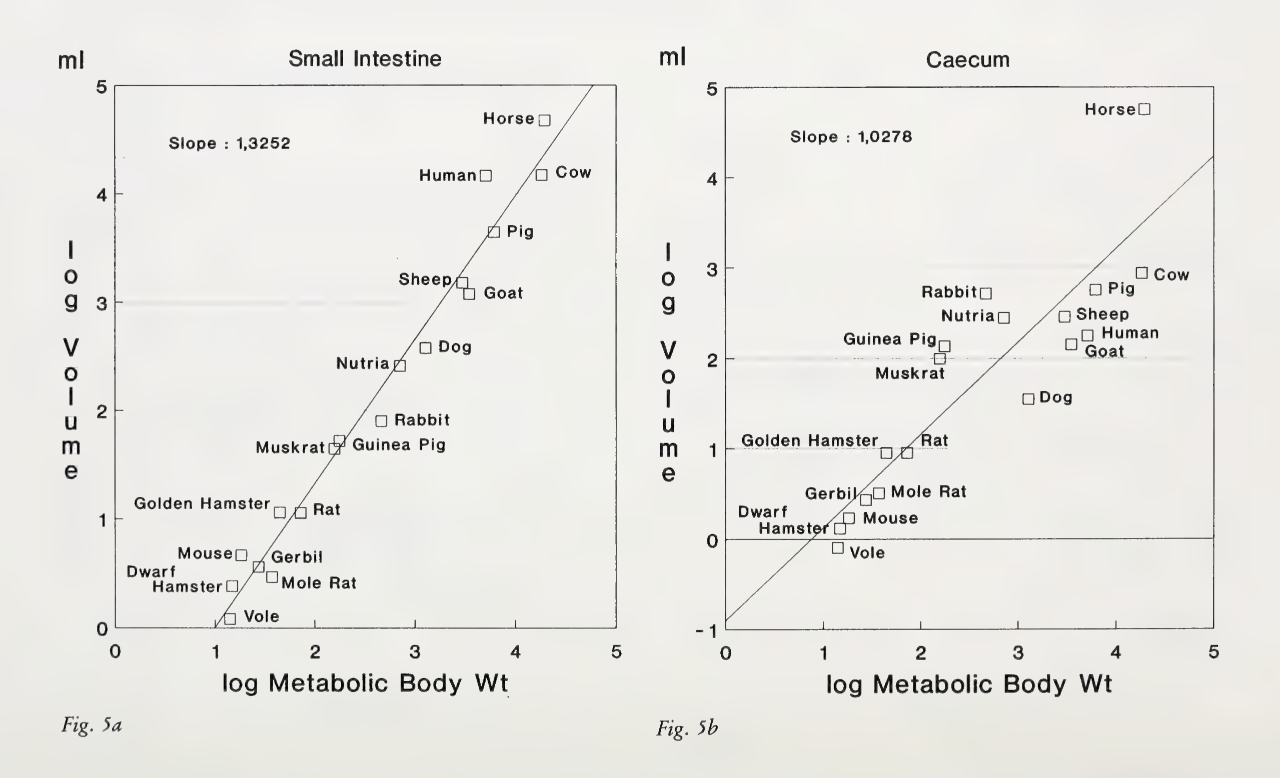

Small Intestine
ml
log Volume
Slope : 1,3252
Horse
Human
Cow
Pig
Sheep
Goat
Dog
Nutria
Rabbit
Muskrat
Guinea Pig
Golden Hamster
Rat
Mouse
Gerbil
Dwarf Hamster
Mole Rat
Vole
log Metabolic Body Wt
Caecum
ml
log Volume
Slope : 1,0278
Horse
Cow
Rabbit
Pig
Nutria
Sheep
Guinea Pig
Human
Goat
Muskrat
Dog
Golden Hamster
Rat
Gerbil
Mole Rat
Dwarf Hamster
Mouse
Vole
log Metabolic Body Wt

Fig. 5a

Fig. 5b

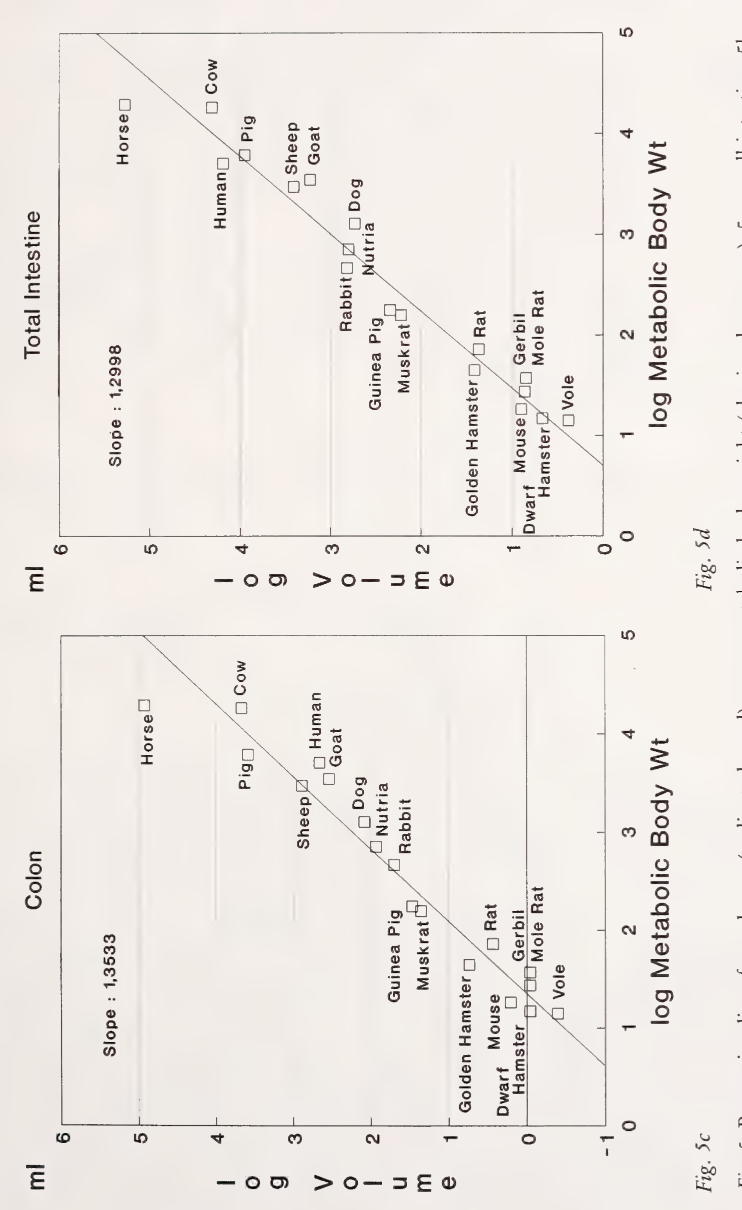


Fig. 5c

Fig. 5d

Fig. 5. Regression lines for volumes (ordinate log ml) versus metabolic body weight (abscissa log grams). 5a: small intestine, 5b: caecum, 5c: colon, 5d: total intestine. Note positive allometry. Coefficients of correlation all significant at the 0.1 % level for this parameter

Coefficients

A convenient method to visualize the area relationships of various animals and to attempt a classification based on the parameter of area is to calculate the "Coefficient of Gut Differentiation" (according to Chivers and Hladik 1980, 1984). This factor results from the ratio area large intestine/area small intestine. In this case large intestine includes the sum of caecum and colon. In Table 2 these values are given (× 100) for both basal areas and total areas. Based on similar values suggested by the above-mentioned authors individual species can be tentatively grouped into one of three dietary adaptations. Large values indicate a substantial functional participation of the large intestine, small values a greater participation of small intestine in the absorptive process. A coarse ranking can be attempted based on these ratios such that all animals with values between 0–30 are classified as faunivores, 30–70 as intermediate feeders and above 70 as herbivores.

Also for volumes a favourable method to analyse volume data is to calculate ratios of: volume large intestine to volumes small intestine (× 10), giving a "Coefficient of Volume" (equivalent to "Coefficient of Fermentation" according to Chivers and Hladik 1980, 1984). Large values indicate a high participation of caecum and/or colon in the fermentation processes (tendency toward herbivory). In Table 3 ratios between 0–7 equal faunivores, 7–15 = intermediate feeders and above 15 = herbivores.

Table 3. **Coefficient of volume**

Presents the ratio of the volume of large intestine divided by the volume of the small intestine

F = Faunivore Rating: 0–7		I = Intermediate 7–15		H = Herbivore 15+	
Human	0.4	Mouse	7.2	Muskrat	27.5
Cow (R)	3.7	D. hamster	9.1	Horse	29.8
Dog	4.1	Vole	9.8	Guinea pig	31.7
Goat (R)	4.1	Gerbil	9.9	Rabbit	71.2
Sheep (R)	7	Pig	9.9		
		Rat	10.1		
		G. hamster	12.5		
		Mole rat	14.1		
		Nutria	14.3		

Large intestine = Caecum + Colon; all values × 10. R = Ruminant.

Area to unit volume relationships

The relation of area to volume is a biologically important and interesting aspect morphometrically. By dividing the area of an intestinal region by its volume the area (cm^2) per unit volume (ml) can give an estimate of the amount of surface area available for absorption. These have been calculated for both basal areas (all 18 species) as well as for total areas (11 species (Table 4). Higher values indicate an advantageous surface area to volume relationship such that absorption is enhanced due to a more auspicous opportunity for digestible material in the lumen to contact the mucosal wall. It is obvious in Table 4 that smaller animals have higher values, i.e., their area/volume relationships are more advantageous than for larger animals, perhaps in correlation to their higher metabolic requirements (slope of regression curves: small intestine −0.38; caecum −0.38; colon −0.28; total intestine −0.41) (graphs not shown).

Table 4. **Area (cm^2) to volume (ml)**

This factor was determined to express the amount of area available in the different compartments of the gut in relation to volume. The ratios were obtained by dividing area by volume. The animals are listed from the smallest to largest according to body weight. Both basal area/volume and total area/volume are given. Smaller animals have higher values, i. e., have a more advantageous relationship of area to volume

Animal	Small intestine		Caecum		Colon		Total intestine	
	Basal/ Vol	Total/ Vol	Basal/ Vol	Total/ Vol	Basal/ Vol	Total/ Vol	Basal/ Vol	Total/ Vol
Vole	12.7	50.3	8.7	15.5	19.1	37.3	12.5	36.8
Dwarf hamster	10.8	28.8	6.3	9.8	13.3	17.3	10.1	21.3
Mouse	10.0	25.7	5.0	9.1	8.3	13.0	8.6	19.5
Gerbil	9.6	24.4	4.2	7.4	13.5	22.5	8.1	12.3
Mole rat	10.6	–	9.6	–	15.9	–	10.8	–
Golden hamster	6.6	25.5	3.9	6.7	9.0	11.8	6.2	16.1
Rat	9.9	22.6	2.9	4.6	8.4	13.9	7.1	14.6
Muskrat	4.6	12.9	1.7	4.3	5.6	11.9	3.0	7.6
Guinea pig	5.8	18.5	1.3	2.9	6.6	10.3	3.1	7.7
Rabbit	5.8	19.5	1.0	2.2	5.3	9.7	1.9	4.9
Nutria	4.1	15.2	1.3	2.4	3.7	7.7	2.8	8.4
Dog	3.0	–	1.7	–	2.1	–	2.7	–
Sheep	4.2	–	1.1	–	3.2	–	3.6	–
Goat	3.2	–	1.4	–	3.9	–	3.2	–
Human	0.6	2.0	0.8	1.5	1.6	3.9	0.6	2.1
Pig	2.3	–	0.8	–	1.4	–	1.8	–
Cow	1.9	–	0.9	–	1.6	–	1.8	–
Horse	0.9	–	0.2	–	0.3	–	0.4	–

Basal = Basal areas; Total = Total areas (Basal area × SEF)

Discussion

The present study has employed modern techniques of morphometry to obtain quantitative data from intestines of 18 mammalian species. The advantages of the present technique include determining the basal areas by measurement of the entire large intestine and not, as previously undertaken, to sample small regions of the large intestine and extrapolate these values to the total length of the large intestine or to determine areas according to formulas by measuring length and breadths (Chivers and Hladik 1980). A second advantage is the use of imagine analysis to determine microscopically visible surface enlargements, which until now have not be included in most studies of intestinal surface area determination.

To interpret morphometric data as a whole (Table 1) it appears expedient to use a linear regression analysis of the individual parameters plotted against metabolic body weight, which is allowed by the distribution of the values. In this way a trend for each aspect can be recognized with respect to differences in body weights. Since the alimentary canal is directly related to satisfying metabolic requirements of the animal, it appears appropriate to use metabolic body weights instead of absolute body weights (Schmidt-Nielsen 1975). By use of the regression lines each individual value can be viewed with respect to this best fitted line, which describes the y of the investigated system with increasing (metabolic) body weight. As mentioned by Martin et al. (1985; see also Stark et al. 1987) not only the trend itself is of biological significance but rather how closely the individual values fit to the line and the subsequent search for a biological significance when a value is distant from the regression line. This aspect will be taken up when such obviously deviant values appear.

Area

The parameter basal area increases with increasing metabolic weight (except caecum) but does not keep pace with an increase in absolute body weight. For the 11 species where histological material was available the basal areas were multiplied by their SEF. Here such important structural entities as villi and plicae circulares for surface enlargement in the small intestine, and mounds, plicae obliquae, folds and "opened crypts" in caecum or colon (SNIPES 1978, 1979a, b, 1981, 1982, 1985; SNIPES and THIELE 1989; SNIPES et al. 1982, 1988, 1990) are taken into consideration. Heretofore, these aspects have been neglected by other investigators. The importance of this type of augmentation can be seen by comparing the basal values with total area values in Table 1. (See SNIPES 1991 for a morphological study of these various anatomical structures.) The regression lines for total areas against metabolic body weight give similar slopes as for basal areas, although direct comparison is not warranted in so far as seven species are not considered in the total area analysis. To make a comparison, slopes were additionally calculated for "basal areas" from only the 11 species that were available for SEF analyses. Slopes for basal areas versus slopes for total areas for the 11 species differ only minimally (for small intestine, respectively, 0.97 vs 1.01; for caecum 0.74 vs 0.77; for colon 0.81 vs 0.89 and total intestine 0.94 vs 1.00).

In each case the regression line for total surface area is closer to isometry. The difference between the two regression lines expresses the degree to which these second-order micro-anatomical enlargements increase the surface area over and above the basal area. The intestinal values for area all show negative allometric scaling to absolute body weight as does metabolim, which surprisingly is in contrast to lung parameters, which scale isometrically with absolute body weight (DUNCKER 1989).

Volume

In the present study volumes were determined from measured basal areas and lengths. Volumes determined by filling with water or other material possess the inherent danger of stretching and over dilating the pliable intestinal walls (CHIVERS and HLADIK 1980). In all cases, regression lines for small intestine, caecum, colon and total intestine (Figs. 5) indicate that volume scales positive allometrically with metabolic body weight (MBW). Thus, the increase in volume for each intestinal region increases slightly more than expected for the body size with increasing metabolic weight. All coefficients of correlation were significant at the 0.1 % level.

With respect to absolute body weight, as expected, all values scale somewhat lower. This is especially true for caecum where the volume versus absolute body weight scales negative allometrically. In this case this may be more in tune with an adaptive situation, and what could almost be expected for a portion of the intestine that is not necessarily tubular or cylindrical such as the other compartments (save stomach). A parallel increase in the caecum could lead to topographical problems in the abdomen in large animals. By close inspection of the graphs it is interesting to note those species divergent from the straight line; notably for caecum: horse, rabbit, nutria, guinea pig and muskrat, are all hindgut fermenters where a large caecum as fermentation vat could be expected; whilst ruminants such as cow, goat and sheep and faunivores (e.g., dog) or "omnivores" (e.g., human and pig) all lie below the line. In the former animals a large caecum for their dietary adaptation (forestomach fermentation) is not required (ULYATT et al. 1975; LANGER 1986; HOFMANN 1989).

Coefficients

The convenient handling of empirical data by transforming to ratios (Tables 2–4) allows a certain ease in surveying the data as well as to discover certain relationships that are not

immediately evident with raw data. Thus, the Coefficient of Differentiation (ratio of area large intestine to area small intestine) gives an indication of surface enlargement to volume in the respective gut compartments of small intestine or large intestine. High values are indicative of a tendency toward herbivory (see Table 2). Based on these high values dwarf hamster, horse, vole, golden hamster, guinea pig, muskrat, mole rat and rabbit can be placed in the category of herbivory. This rating correlates well with a highly developed large intestine (caecum and/or colon) possessing well-differentiated internal structures in these species (Luppa 1961; Snipes 1978, 1979a, b, 1982; Snipes et al. 1990). It is interesting to note when comparing the ratios for basal areas to the ratios for total areas in each animal a lower coefficient is found for the latter. This results from the proportionally much larger microscopically visible surface enlargements in the small intestine (villi, plicae circulares) than found in the large intestine (compare also SEF values in Table 1). The total areas (basal × SEF) give a more realistic value for the situation in the gut. Basal areas are also given here since to our knowledge all comparative investigations to date have used only basal areas or their equivalents. Note that ruminant forms (sheep, goat, and cow) possess values in the faunivore or lower intermediate ranges. The role of the hindgut in ruminant digestion has been discussed by Janis (1976), Ulyatt et al. (1975) and Hofmann (1989).

The equivalent ratios for volumes (volume large intestine/volume small intestine) (Table 3) give a Coefficient of Volume and affords perhaps a better indication of herbivory than the previous coefficient for area. According to this criterion the following species qualify as herbivores: muskrat, horse, guinea pig and rabbit. This classification appears to be somewhat more restrictive. Note here that ruminants show lower values and range again with faunivores. Again this is not surprising since they possess a complicated and voluminous forestomach for their fermentation function.

The intermediate classification contains the largest number of animals. Nutria, golden hamster and mole rat border on values to herbivory and at least in the case of nutria and mole rat the dietary strategy and morphological aspects of the caecum are reminiscent of herbivory. The morphological aspects of the latter species' intestines speak for their inclusion in the category "herbivory" (nutria: Wagner 1963; Kämmerer and Wetzig 1966; Stahl 1987; Snipes et al. 1988; mole rat: Snipes et al. 1990). Borderline values such as these indicate that the classification should not be held rigid but rather should be looked upon as a continuum and as a dynamic concept. For want of a better designation, "intermediate" at least allows classifying animals with varied dietary types and it is preferable to the older term "omnivore". The rat (Sperber et al. 1983; Snipes 1981) (perhaps also pig) may be an example of a "true" omnivore. The other members of the intermediate group (especially gerbil, hamster, vole) often show changes in dietary habit in adaptation to seasonal, climatic, environmental and ambient conditions and are better placed in a neutral classification denominated "intermediate". Volume coefficients give a relatively good indication of the presence of a large fermentation vat in the hindgut (either caecum and/or colon) as substantiated by the well-known anatomy of the large intestine of horse (Chivers and Hladik 1980), rabbit (Snipes 1978), guinea-pig (Gorgas 1967; Snipes 1982) and muskrat (Luppas 1961).

Area to unit volumes

The area to volume ratios give an impression of the amount of area available within a compartment of the intestine in relation to its volume. Granted, large animals have greater intestines and therefore empirically more surface area, but relatively seen by use of this ratio the relationship changes to the advantage of the smaller animals.

In voluminous sacs such as large caeca in some herbivores the situation could tend to become disadvantageous for the contact of digesta with mucosal wall, unless a special anatomical adaptation is introduced to increase the area to volume relationship. In both the

rabbit (Snipes 1978) and mole rat (Snipes et al. 1990) a spiral fold courses throughout the entire caecum and increases the surface area several fold and thus enhances the contact possibility of intestinal wall and luminal content. This unit factor appears to be correlated more closely with body weight than with dietary type. It is obvious that small animals have more advantageous surface to volume relationships (Table 4). This could correlate with the higher metabolic rates in small animals and their correlative higher energy requirements which must be fulfilled by a more efficient absorption (possibly through advantageous surface to volume relationships).

By comparing the ratios gained for basal area/volume with values for total area/volume for each intestinal portion certain tendencies become apparent. The ratios increase from basal to total areas in all regions of the intestine as would be expected (that portion due to micro-anatomical enlargements) but to differing degrees. For example, the differences for small intestine are greater than for large intestine (caecum and colon). This evidently reflects the greater dimension due to villi in the small intestine compared to such enlargements in the large intestine (widened crypts, folds, mounds; Hladik 1967; Snipes 1991). These differences again reflect the amount of the SEF factor in each region. (See Table 1).

Studies are in progress to advance the morphometrical analysis to the ultrastructural level to account for the surface area enlargement due to microvilli.

Granted, many other factors also play decisive roles in the different dietary adaptations. One important aspect is the transit time of gut content through the intestine (Warner 1981; Langer 1991; Langer and Snipes 1991).

Another important factor when considering surface area relationships is the presence of the glycocalyx and the mucus layer covering the mucosa (Sakata and v. Engelhardt 1981). Moreover, the true diffusion factor of digestible material through the mucosal wall must take into consideration similar factors that have been determined for the lung (Duncker 1989), namely, an anatomical diffusion factor.

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Zusammenfassung

Quantitaive Untersuchung an Gesamtoberfläche und Volumen verschiedener Darmabschnitte von 18 Säugetierarten

Untersucht wurden morphologische Parameter des Dünn- und Dickdarms von 18 Säugetierarten. Eine neue Methode wird beschrieben, mit der mittels Planimetrie Gesamtoberflächen von Darmabschnitten bestimmt wurden. Zusätzlich wurde ein Computer-unterstütztes Programm benutzt, mit dem auf lichtmikroskopischem Niveau die Vergrößerung der Oberfläche der Darmschleimhaut bestimmt werden kann. Hiermit wird ein Oberflächenvergrößerungs-Faktor festgestellt, welcher, mit den planimetrisch ermittelten Werten multipliziert, den Gesamtwert der Oberflächenvergrößerung des jeweiligen Darmabschnitts angibt. Die Daten werden in Koordinatensystemen dargestellt und zur Berechnung linearer Regressionen verwendet. Die Ergebnisse zeigen sehr deutlich, daß die Binnenflächen des Dünndarms, des Colons und des Gesamtdarms nahezu isometrische Beziehungen zum metabolischen Körpergewicht zeigen, während das Cäcum negative allometrische Beziehungen aufweist.

Der Quotient aus Gesamtfläche und Volumen der betrachteten Darmabschnitte bietet eine Vorstellung über die Binnenfläche, die pro Volumeneinheit verfügbar ist. Kleinere Säuger haben pro Volumeneinheit eine relativ größere Binnenoberfläche als große. Dieser Befund wird auf die höhere Stoffwechselrate der kleineren Säuger zurückgeführt.

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WISSENSCHAFTLICHE KURZMITTEILUNGEN

Ein Fund des pliozän/pleistozänen Marderhundes *Nyctereutes megamastoides* (Pomel, 1843) in Österreich

Von K. Bauer

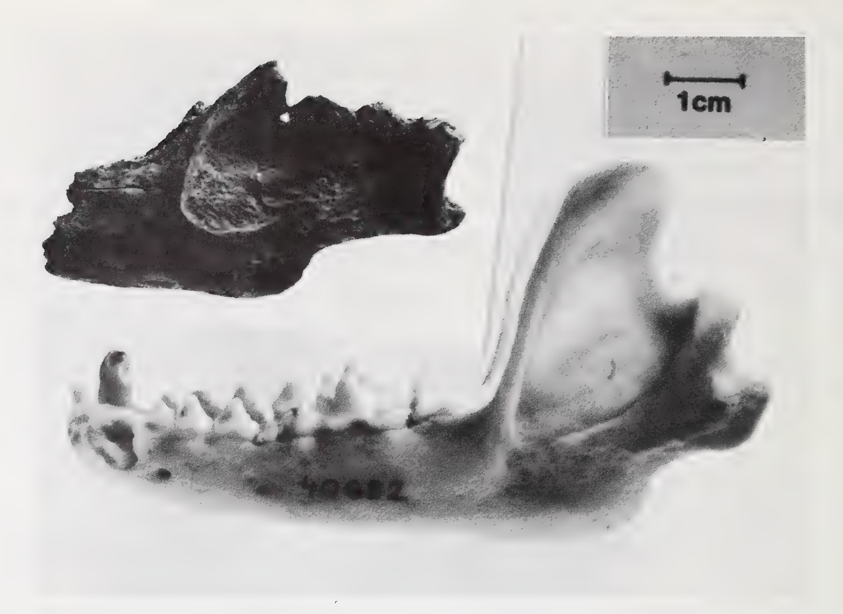
Archäologisch-zoologische Sammlung des Naturhistorischen Museums, Wien, Österreich

Eingang des Ms. 17. 1. 1991
Annahme des Ms. 25. 2. 1991

Am 12. Mai 1985 sammelten die Mitglieder des Landesvereins für Höhlenkunde in Wien und Niederösterreich M. Häusler† und E. Hermann in der Westlichen Hubberghöhle (Nr. 1873/3 des österr. Höhlenkatasters) im Gebiet der Gemeinde Ybbsitz/Bezirk Amstetten, Niederösterreich (sub)rezente Beutereste von Schleiereule oder/und Uhu (H 90–83). Neben dieser faunengeschichtlich interessanten jungholozänen Faunula (u. a. Hamster *Cricetus cricetus* und Hausratte *Rattus rattus*, die gegenwärtig im Bezirksgebiet nicht bzw. nicht mehr vorkommen) fanden sich in der Aufsammlung bei ihrer Auswertung im Dezember 1990 drei mitaufgelesene Bruchstücke fossiler Säugetierknochen. Ein kleiner, ziemlich vollständiger Lumbalwirbel und das Bruchstück einer (Humerus)Diaphyse sollen hier nicht weiter interessieren. Eine linke Mandibel ist zwar nur ganz fragmentarisch erhalten, aber aussagekräftiger. Das 55 mm lange Bruchstück weist neben den leidlich erhaltenen Processus articularis und angularis und dem unteren Teil der Fossa masseterica eine intakte Unterkante auf und zeigt dort einen sehr auffälligen Doppelknick („subangular lobus“, Clutton-Brock et al. 1976). Dieses recht ungewöhnliche Merkmal deutet auf die Canidengattung *Nyctereutes* hin, und der Detailvergleich mit rezentem Material bestätigt eine solche Zuordnung (Abb.).

Nyctereutes ist rezent in einer Art *(N. procyonoides)* in Ostasien autochthon sowie in neuerer Zeit dank menschlicher Hilfe auch über Ost- und Mitteleuropa verbreitet. Im Pliozän kam die Gattung westwärts bis zur Iberischen Halbinsel vor, und etwa um die Pliozän/Pleistozän-Wende erschien sie vorübergehend sogar im südlichen Afrika (*N. terblanchei* [Broom]; Ficcarelli et al. 1985). Auf die älteste frühpliozäne Art *N. donnezani* folgte im mittleren Pliozän die paläarktisch verbreitete Art *N. megamastoides*. *N. megamastoides* erlosch in Europa im Villafranchium, überlebte in der (insgesamt anscheinend etwas jüngeren) östlichen Subspezies *N. m. sinensis* in China aber bis in das Mittelpleistozän und wurde dort zur Stammform der erstmals in jungpleistozänen Schichten von Choukoutien nachweisbaren lebenden Art *N. procyonoides* (Pei 1934; Kurtén 1968; Soria und Aguirre 1976). *N. donnezani* ist größer und hat einen gröberen, stark gerundeten Subangularlobus. *N. megamastoides* dagegen stimmt, von etwas größeren Dimensionen abgesehen, strukturell weitgehend mit *N. procyonoides* überein. Nach den von Pei (1934), Viret (1954) und Soria und Aguirre (1976) zusammengestellten Photos und Zeichnungen handelt es sich beim vorliegenden Stück um *N. megamastoides*. Zoologische oder paläontologische Standardmaße können an dem Fragment nicht gewonnen werden. Die Strecke vom Zusammentreffen der bei den fossilen und rezenten Formen die Fossa masseterica in der Regel scharfkantig begrenzenden Cristae mandibulae oralis und aboralis bis zur Bucht zwischen den Processus angularis und articularis beträgt bei 6 zum Vergleich verfügbaren rezenten adulten Stücken der Säugetiersammlung des Naturhistori-

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Fragmentarische linke Mandibel von *Nyctereutes megamastoides* aus der Westlichen Hubberghöhle bei Ybbitz, Niederösterreich. Zum Vergleich ein sehr kräftiges Stück von *N. procyonoides* (NMW 40882) aus Masuren/NO-Polen (Photo: Alice Schmumacher)

schen Museums aus Japan, Russisch Fernost, Polen und Österreich (NMW 998, 1110, 40517 und 40880-82), die recht gut die erhebliche Größen- und Formvariation innerhalb von *N. procyonoides* abdecken, 22,0–30,4 mm, beim angesichts seiner überaus plastischen Strukturierung gleichfalls adulten Fossil (NMW H 90-83-21) 33,5 mm.

N. megamastoides (in der Umgrenzung von Soria und Aguirre 1976) ist bisher aus Spanien, Frankreich, Italien, Griechenland, Polen, Ungarn, Rumänien, Ukraine, Grusinien, Tadschikistan und Israel sowie aus Transbaikalien, Mongolei und China und in Europa aus Straten vom Pliozän bis zum Altpleistozän bekannt geworden (Soria und Aguirre 1976; Baryschnikow 1981; Scharapow 1981), und mindestens altpleistozänes Alter wird auch für den vorerst nicht datierbaren Neufund anzunehmen sein.

Über seinen kleinen Beitrag zur Paläofaunistik hinaus hat unser Zufallsfund eventuell als Hinweis auf eine erste jungtertiäre oder altpleistozäne Fossilfundstelle im diesbezüglich bisher fundleeren südwestlichen Niederösterreich gewisse Bedeutung. Die Beschreibung der kleinen, wie eine Nachbarhöhle etwa im 18. Jahrhundert durch einen Steinbruch aufgeschlossenen, aber nur durch Abseilen erreichbaren und deshalb ungestört gebliebenen Höhle in einer von einer Reihe von Jurakalk-Klippen in den Flyschvoralpen (Herrmann et al. 1985; Hartmann und Hartmann 1985; s. auch Thenius 1974) deutet auf Paläokarst mit Spaltenfüllungen hin, die zu eingehenderer Sondierung einladen.

Der holozäne Anteil der Aufsammlung H 1990–83 ist in der faunistisch-faunengeschichtlichen Sammlung der Säugetiersammlung des NMW archiviert, die Fossilreste wurden an die Paläontologische Abteilung weitergegeben.

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First record of a fossil *Cervus elaphus* L., 1758, from Albania

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In 1978 a fragment of a fossil deer skull was discovered at a depth of 1.5 metres in peaty sediments of the Tarovica swamp near Lezhë, South of Shkodër in N. W. Albania, during drainage work. Initially placed in the Lezhë Ethnographical Museum, it is now inscribed in the collection of my laboratory as number 78/1.

The Tarovica swamp between Bushati and Lezhë near the Adriatic coast is several kilometres long and lies a few hundred metres above present sea-level between the North-to-South running mountain ranges of Rrenci-Barbullushi (nearest the coast) and Köles-Kakarriqi. Its peaty sediments overlie lowermost Tertiary Nummulitic, and Cretaceous Rudist limestones. Quaternary sediments such as this peat are present in many Albanian areas (Bourcart 1919, 1925; von Nopsca 1929; Nowack 1929). Until now no fossil remains of large mammals appear to have been recorded from these areas.

The fossil in question is a relatively well-preserved, but recently damaged skull fragment (Fig. 1) consisting of an incomplete neurocranium with partially preserved antlers. The left antler is broken off at the base of the bez (or second tine); the tip of the browtine (first tine) is absent. The right antler's beam is broken near the base of the fourth tine; tips of the browtine and bez are no longer present. The cranial bone has a chestnut-brown colour with cream-coloured spots. Outer surfaces of warts and pearls are off-white. The dirty rust-brown colour of the deeper parts of the antlers has undoubtedly been caused by humic acids from the peat.

A sample of a few milligrammes from the antlers and the skull was used for quantitative nitrogen analysis according to the Kjeldahl method. It was carried out with the idea (Cantaluppi 1973; Fistani 1988) that the break-down of bone matrix as a reflexion of age of a fossil can be expressed as a decrease of its nitrogen content. The Tarovica specimen gave a result of 2.069 % N. An Upper Pleistocene age does therefore not seem impossible.

The occipitalia in the skull fragment are well preserved (Fig. 1; 4). Occipital width exceeds height, indicating a strong individual. The upper edge of the nuchal linea forms a ridge. The complete long axes through the occipital condyles form angles of about 45° with a horizontal line through the foramen magnum. An occipital torus separates the left and right supra-occipital regions. The outline of the foramen magnum at the junction of the condyles with the basi-occipital (Fig. 1; 3) is similar to that described by Kotsakis et al. (1978) for *Cervus rianensis* and apparently different from that in (most) red deer. The two condyles form an angle of ± 90° with each other in the Tarovica and Riano specimens. Some cranial and antler measurements ot the Albanian specimen are given in Table 1.

The tympanic bullae are distinctly separate from the fused basi-occipital/basi-sphenoidal, typical for *C. elaphus*, although there exists a considerable degree of individual morphological variation. The Tarovica fossil has a large, flat, rugose area near the acoustical porus and differs in this respect from the specimen in Fig. 26 in the monograph by Flerov (1952).

The considerable distance between occipital arc and shortest length between the two pedicels attests to the robusticity of the fossil. Fronto-parietal sutures are fused. The

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frontal suture midway between the pedicels is partly synostosed. The Tarovica animal therefore attained a fairly high age. Seen from behind (Fig. 1; 4) the two pedicels form an angle of approximately 95° with each other. Each one has an almost ovoid cross-section. Their height is surpassed by that of *Cervus* specimen no. 636 from Torre in Pietra (PALOMBO, in CALOI 1978). Left and right browtines stand parallel to each other and to the sagittal axis of the skull. The edge of each burr forms a wavy plane (Fig. 1; 1). The stout burrs contrast with the relatively thin pedicels. The very high value for the beam/browtine angle again underlines the robusticity of the Tarovica specimen.

BOUCHUD (1972) warned against proposing a separate subspecies when only scanty material is available. Bearing this in mind there is no good reason to go beyond a general identification of the Tarovica find as *Cervus elaphus* Linnaeus, 1758. It was a very large, robust and healthy animal, living under optimal conditions.

Some authors are of opinion that a progressive increase in size can be observed among red deer from the Lower to the Upper Pleistocene (for example VERESHTCHAGIN 1959 or PRAT and SUIRE 1971). Others (see ERDBRINK 1964 for a compilation) conclude that European fossil *C. elaphus* were neither stronger nor larger than recent red deer. Large size is only a result of optimal ecological conditions, expressed by measurements such as the



Fig. 1. Incomplete skull of *Cervus elaphus* L., Tarovica, Albania. 1: Right lateral aspect; 2: Aspect from above; 3: Aspect from below; 4: Aspect from behind. (Bars: 10 cm)

Table 1. **Cranial and antler measurements of *C. elaphus* L. from Tarovica, no. 78/1**
Measurements in mm

Occipital height	94.0
Occipital width	147.4
Width between condyles	72.7
Sagittal diameter of foramen magnum	33.0
Transverse diameter of foramen magnum	31.0
Transverse width of skull between parieto-temporal sutures	111.0
Minimum external width between pedicels	170.0
Minimum internal width between pedicels	54.0
Transverse width between upper orbital edges	117
Distance between supraorbital foramina	87.2
Maximum diameter of supraorbital foramen	9.5
Remaining length of right beam	420
Hypothetical length of entire right antler	580–600
Cross-section of right beam at base, sagittal × transverse	48.0 × 48.7
Cross-section of right beam at 150 mm above burr, sagittal × transverse	45.6 × 45.0
Cross-section of right browtine, sagittal × transverse	39.4 × 35.0
Cross-section of trez (3rd tine), sagittal × transverse (dextra)	40 × 32
Height of pedicel	dext. 30.5; sin. 29.4
Anterior posterior diameter of pedicel	dext. 49.3; sin. 51.5
Transverse diameter of pedicel	dext. 47.7; sin. 48.1
Anterior posterior diameter of burr	dext. 82.6; sin. –
Transverse width of burr	dext. 74.5; sin. 73.2
Length of browtine along upper incurvation	dext. 270.0; sin. 230.0
Angle between beam and browtine	dext. 136°; sin. –

angle between beam and browtine. Application of Bergmann's rule (1847) is not necessary in order to explain the large size of a red deer by supposing that it lived during a cold phase of the Pleistocene. On the other hand, such an influence should not be ruled out either.

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Archaeological evidence of *Pudu pudu* (Cervidae) in central Chile

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Pudu pudu is the smallest South American deer. Normally, their head and body length measures approximately 800 mm, the height of the shoulder 400 mm, typically the weight less than 10 kg. Males bear a spike-like antler. *Pudu pudu* is endemic to forest regions of south-central Chile, inhabiting dense forest and bamboo patches (Osgood 1943; Nowak and Paradiso 1984; see Hershkovitz 1982 for a review of the genus). In Chile, *P. pudu* occurs from Curicó (35° S) southward, exhibiting a more continuous distribution south of Bio Bio down to northern Magallanes (46° S app; Tamayo and Frassinetti 1981). However, it is presumed that *P. pudu* formerly extended their distribution further north, but there is no evidence to support this assumption. Further, it is assumed that *P. pudu* disappeared from northern areas only recently (Miller 1980).

During the recovery of faunal remains from archaeological sites in the foothills of the Andes of Santiago, we found a specimen attributable to *P. pudu*. Here, we describe this finding.

The remain was recovered from an excavation at La Batea 1 rockshelter, located in the El Manzano creek, Maipo River (33° S). The site is located at 1250 m above sea level in the foothills of the Andes of Santiago. This site was used by prehistoric humans from 5560 ± 250 to 1430 ± 280 B.P. as a stopover refuge while in transit from the lowlands to the higher mountains (Cornejo and Simonetti 1990). The remnant was recovered among faunal remains from other mammals, including rodents and camelids. The single piece attributed to *P. pudu* is the lower portion of an eroded antler, which was recovered from stratum 5, dated 2390 ± 130 B.P. The specimen comprises the burr and a small portion of the beam. The diameter at the base is 9.7 to 8.0 mm, and the beam has a strong angulation toward the back (141°), typical features of *Pudu* antlers. The specimen is labeled B1 EC1 (C2) N7 in the temporary collection of the Chilean Museum of Precolumbian Art at Santiago.

Archaeofaunal specimens employed as an attribute of an archaeobiological sample can be used confidently to assess the presence of a given animal species in a region (e.g., Grayson 1983). In our case, the single antler recovered gives support to the previous contention that *P. pudu* may have had a wider distribution in the recent past (Miller 1980). The paucity of the archaeological and paleontological records precludes any analysis regarding the speed and potential causes of their disappearance from the Andes of Santiago. The single record dates from the late Archaic period, when human populations exploited the Andean region only seasonally, prior to the advent of native agriculture and presumed habitat alteration that could have diminished *P. pudu* populations (Miller 1980; Cornejo and Simonetti 1990). Further, the scarcity of records could also reflect the rarity of this species in central Chile due to lack of suitable habitat following the last glacial period (Miller 1980). The disappearance of another cervid, *Hippocamelus bisulcus* from north-central Chile during the Holocene may give some support to this argument. *Hippocamelus* is currently distributed much like *Pudu* in south-central Chile, but during the late

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Pleistocene reached the 31° S (SIMONETTI 1990 for a review). Both *Pudu* and *Hippocamelus* may have restricted their distribution following the vegetational changes that followed the last glacial period (e.g., HEUSSER 1983).

Reference osteological collections of *P. pudu* are almost non-existent in Chilean museums (YÁÑEZ 1982). This fact may have precluded the analysis of faunal remains from archaeological sites. Fortunately, *Pudu* remains can be distinguished from other cervids because the cuneiform is fused with the navicular/cuboid, rendering a key element to determine the presence of this species in the archaeological record. Undoubtedly, a careful reexamination of bones from large mammals recovered in central Chile is urgent, as it may clarify past and present distributional patterns of the mammalian fauna.

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Anomalies of the upper incisors in the genus *Microtus* (Cricetidae, Rodentia)

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Tooth anomalies of the upper incisors have been reported for *Microtus richardsoni* (Russell and Anderson 1956), *M. pinetorum* (Fish and Whitaker 1971) and *M. longicaudus* (Jones 1978). In all these cases deep medial grooves on the anterior surface of the upper incisors were present, and frequencies of these aberrations within samples were low, ranging from 1.6 % in *M. richardsoni* (n = 60) to 2.5 % in *M. pinetorum* (Jaeck and Jones 1990).

The following five infrequent anomalies of the upper incisors were observed in a survey of 3765 specimens from 27 microtine species. These aberrations occurred either on both or only on one of the upper incisors:

1. double grooves: two narrow, parallel grooves slightly lateral on the anterior surface, extending the whole length of the incisor.
2. medial grooves: deep (0.5 mm in one specimen of *M. richardsoni*), narrow grooves running medial on the anterior surface of the tooth.
3. constrictions: incisor shows circular constrictions, irregularly spaced on its entire length. Constrictions are continuous around the tooth.
4. "undulations": shallow circular depressions occurring in short regular intervals along the entire length of the incisor, giving the anterior surface an undulated appearance.
5. "curled tips": cutting edge of incisor is not straight, but the outer edges are „curled" towards the lingual side of the tooth, giving it a hollowed appearance when looking down onto its tip.

Within the species *M. agrestis, M. ochrogaster, M. pennsylvanicus* and *M. richardsoni*, 22 individuals exhibited these anomalies as is summarized in the table.

Numbers of anomalies found in four species of *Microtus*

Anomaly		*Microtus*			
		agrestis	*pennsylvanicus*	*ochrogaster*	*richardsoni*
	n	131	2599	160	107
Double grooves		–	5 b	1 f	2 g
Medial groove		1 a	2 c	–	6 h
Constrictions		–	2 d	–	–
Undulations		–	–	–	1 i
Curled tips		–	2 e	–	–

a: USNM 85902; b: NUVC 2215, 2216, 2217, 2218, 2229; c: NUVC 2214, 2228; d: NUVC 2224, USNM 76256; e: NUVC 2226, USNM 268327; f: ISU 4330; g: USNM 230457, 233198; h: USNM 233187, 233194, 233196, 233204, 81379, 174470; i: USNM 74261.
ISU = Indiana State University; NUVC = Northeastern University Vertebrate Collection; USNM = United States National Museum.

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In one specimen of *M. pennsylvanicus* (USNM 76256), which had constrictions on the upper incisors, only the left tooth exhibited this anomaly in combination with atrophy, whereas the right incisor was not mis-shaped and of normal size. The medial groove in NUVC 2214 (*M. pennsylvanicus*) and the double groove in USNM 233198 (*M. richardsoni*) were interrupted by one or two short gaps, respectively.

Grooves on the upper incisors of *M. pennsylvanicus* and other microtines have only recently been reported to be a regular characteristic within the microtines (JAECK and JONES 1990). The tooth anomalies dealt with in the present paper do not correspond with those regular forms of grooves, but rather are rare aberrations.

The development of these anomalies remains open to speculation. For the constrictions on the incisors, malnutrition and consequent underdevelopment of the tooth cannot be a possible cause, since some specimen exhibit one normal and one deformed tooth. If malnutrition was the cause, both incisors would be affected. Double and medial grooves are probably caused by irregularities of the alveolar cavity, impressing themselves onto the developing tooth.

It is important to note that particularly grooves not only are a key character in many rodent genera (e.g. *Zapus, Reithrodontomys, Synaptomys*), but can also occur "accidentally" in taxa not noted for exhibiting them.

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The author thanks ROBERT FISHER, U.S. National Museum of Natural History, Washington D.C., JOHN O. WHITAKER, Jr., Indiana State University, TERRE HAUTE, and GWILYM S. JONES, Northeastern University Vertebrate Collection, Boston, for access to their respective collections. RALPH R. KUNKEL and GWILYM S. JONES critically read the manuscript and provided many helpful comments.

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BUCHBESPRECHUNGEN

Bronson, F. H.: **Mammalian reproductive biology.** Chicago, London: The University of Chicago Press 1989. 325 pp., 54 figs, 4 tables, US $ 20,75, £ 14,25 (brosch.), US $ 51,75, £ 35,95 (geb.). ISBN 0-226-07558-3 (brosch.), 0-226-07559-1 (geb.)

Das Buch möchte die Beziehung zwischen den bei den Säugetieren sehr unterschiedlichen Fortpflanzungsweisen und den Umweltbedingungen darstellen. Die Umwelt wirkt ultimat, indem sie zu bestimmten Reproduktionsstrategien führt, beeinflußt aber auch proxiat etwa über das Nahrungsangebot und die Temperatur das jeweilige Fortpflanzungsgeschehen. Eine Fülle von Arbeiten vor allem aus den letzten 20 Jahren hat hier eine geradezu unüberschaubare und dennoch vielfach noch unzureichende Menge an Erkenntnissen gebracht. So ist inzwischen in vielen Fällen durch kontinuierliche Messung von Hormonkonzentrationen die hormonale Steuerung recht gut geklärt, und auch der Einfluß von Umweltparametern wurde hier deutlich erfaßt. Die Säugetiere können in ihrem Fortpflanzungsverhalten auf Umwelteinflüsse in der Weise „zweckmäßig" reagieren, daß sie diese auf günstige Perioden beschränken. Bei regelmäßigen jahresperiodischen Änderungen können sie Umweltänderungen wie in der Fotoperiode aber auch als Zeitgeber benutzen, die das wahrscheinliche Eintreten günstiger Bedingungen vorhersagen. Schließlich können Artgenossen über Pheromone die Fortpflanzungsfähigkeit beeinflussen. Da die Umweltbedingungen im Verbreitungsgebiet einer Art häufig variieren, ändert sich auch das Fortpflanzungsverhalten geographisch erheblich, wie die Karten 3.3–3.5 eindrucksvoll zeigen. Der Autor betont deshalb, daß eigentlich nur für Populationen einheitliche Reproduktionsmuster angegeben werden können, nicht aber für Arten.

Als Verdienst dieses Buches ist also hervorzuheben, daß es eine Synthese zwischen ökologischen und physiologischen Komponenten erreicht. Es stützt sich auf ein 81 Druckseiten beanspruchendes Literaturverzeichnis, das ganz überwiegend Arbeiten aus den beiden letzten Jahrzehnten bis 1988 (freilich fast ausschließlich englische) enthält. Schließlich bietet es eine Reihe klarer und doch nicht zu einfacher Diagramme. Nicht behandelt werden die Steuerung der Wurfgröße, das Zustandekommen zyklischer Massenvermehrungen und weitergehende soziobiologische Aspekte der Fortpflanzung. Schwächen finden sich im taxonomischen Bereich. So wird *Elephantulus* noch bei den Insektenfressern abgehandelt, die Pinnipedia sind eine eigene Ordnung. Ziemlich viele wissenschaftliche Artnamen enthalten Schreibfehler, und im Index ist *Peromyscus* der einzige lateinische Name.

Trotzdem: Von kleinen Mängeln abgesehen, ist dies ein sehr inhaltsreiches, informatives und anregendes Buch, das nicht nur einen guten Einblick in sein verwickeltes Thema bietet, sondern auch einen ausgezeichneten Schlüssel zur zugehörigen modernen Literatur liefert. Interessenten kann es nur nachdrücklich empfohlen werden.

J. Niethammer, Bonn

King, C. M.: **The natural history of weasels and stoats.** London: Christopher Helm 1989. 253 pp., num. figs. and tables. £ 15.95. ISBN 0-7470-1800-6

In this book the internationally well-known mustelid expert Carolyn M. King has summerized both new and previous knowledge on weasel and stoat biology. The content is presented in 14 chapters headlined: introduction; hair-trigger mousetraps with teeth; moult and winter whitening; body size; food; hunting behaviour; impact of predation by weasels on populations of natural prey; adjustable living spaces; reproduction; population density; productivity, lifespan and mortality; delayed implantation; sexual dimorphism and co-existence among weasel species; weasels and man; general summary.

Although mainly dealing with *Mustela nivalis* and *M. erminea* some results on other species of *Mustela* are additionally mentioned. In general, weasels and stoats are fully and well described. Some interesting species-characteristic peculiarities, and biological phenomena are especially discussed in greater detail (extreme sexual dimorphism, unusual broad size and colour variability, delayed implantation versus uninterrupted development, "infant-pregnancy" in female stoats from an age of 17 days on, etc.). Furthermore, the author has included valuable results on what may be called from a biological point of view the "New Zealand experiment". Thus, it is documented again that after having been introduced by man common weasels definetely have not thrived in New Zealand, whereas stoats show a much broader range of ecological adaptiveness through an explosive increase in population. Moreover, concerning several morphological traits this latter specis has developed in New Zealand within less than 100 years a range of variation comparable to that recognized through the whole of continental Europe.

The book is well written if not in some chapters rather too detailed. Moreover, there is a wealth of summarizing figures and tables. The pure descriptions of facts are often supplemented by anecdotes and personal adventures, and several repetitions doubtlessly occur. However, it is an excellent source of information on the topic and highly valuable for both the specialist of mustelid biology as well as for the layman.

D. Kruska, Kiel

Subscription information for USA, Canada and Mexiko obtainable from Paul Parey Scientific Publishers, PO Box 1815, 150 East 27th Street, # 1 A, New York, NY 10156-0610, USA. Phone and Telefax (212) 213-3798.

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EITSCHRIFT FÜR SÄUGETIERKUNDE

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Die Zeitschrift für Säugetierkunde veröffentlicht Originalarbeiten und wissenschaftliche Kurzmitteilungen aus dem Gesamtgebiet der Säugetierkunde, Besprechungen der wichtigsten internationalen Literatur sowie die Bekanntmachungen der Deutschen Gesellschaft für Säugetierkunde. Verantwortlicher Schriftleiter im Sinne des Hamburgischen Pressegesetzes ist Prof. Dr. Dieter Kruska.

Zusätzlich erscheint einmal im Jahr ein Heft mit den Abstracts der Vorträge, die auf der jeweiligen Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde gehalten werden. Sie werden als Supplement dem betreffenden Jahrgang der Zeitschrift zugeordnet. Verantwortlich für ihren Inhalt sind ausschließlich die Autoren der Abstracts.

Manuskripte: Manuskriptsendungen sind zu richten an die Schriftleitung, z. Hd. Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Biologie-Zentrum, Neue Universität, Olshausenstr. 40–60, W-2300 Kiel, Bundesrepublik Deutschland. Für die Publikation vorgesehene Manuskripte sollen gemäß den „Redaktionellen Richtlinien" abgefaßt werden. In ihnen finden sich weitere Hinweise zur Annahme von Manuskripten, Bedingungen für die Veröffentlichung und die Drucklegung, ferner Richtlinien für die Abfassung eines Abstracts und eine Korrekturzeichentabelle. Die Richtlinien sind auf Anfrage bei der Schriftleitung und dem Verlag erhältlich.

Sonderdrucke: Anstelle einer Unkostenvergütung erhalten die Verfasser von Originalbeiträgen und Wissenschaftlichen Kurzmitteilungen 50 unberechnete Sonderdrucke. Mehrbedarf steht gegen Berechnung zur Verfügung, jedoch muß die Bestellung spätestens mit der Rücksendung der Korrekturfahnen erfolgen.

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Rückverlagerte Choanen und akzessorische Bulla tympanica bei rezenten Vermilingua und *Eurotamandua* aus dem Eozän von Messel (Mammalia: Xenarthra)

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Eingang des Ms. 22. 4. 1991
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Abstract

Posteriorly displaced internal nares and supplementary auditory bulla in extant Vermilingua and Eurotamandua from the Eocene of Messel (Mammalia: Xenarthra)

X-ray examination of the type skeleton of *Eurotamandua joresi* from the middle Eocene of Grube Messel, Hessen, Germany, revealed two striking skull features: 1. Like in extant anteaters, the pterygoids are considerably expanded posteriorly, and they form horizontal palatal plates; the internal nares are thus displaced close to the foramen magnum (= autapomorphic character of the suborder Vermilingua). 2. Like in extant *Tamandua* and *Myrmecophaga,* there is a supplementary bulla tympanica in front of the tympanic cavity (= autapomorphic character of the family Myrmecophagidae). Both characters are obviously correlated with ant- and termite-eating: The elongate hard palate supports the convey of food items to the pharynx and forms a partition wall for the nasal cavity; the hypotympanic sinus most likely is an acoustic adaptation for percussion of hard termite nests and probably acts as Helmholtz resonator. The osteology of the auditory and pterygo-alisphenoid regions of extant Vermilingua is described, differences between *Eurotamandua* and *Manis* (Pholidota) are enumerated, and a classifcation of the Vermilingua is proposed. Anteaters must have diverged from a common xenarthran stem very early, i.e. well back in the Cretaceous. The basal dichotomy within Vermilingua into Myrmecophagidae and Cyclothuridae, too, most probably occurred in Cretaceous times.

Einleitung

Eurotamandua joresi Storch, 1981 aus dem Mittel-Eozän Deutschlands ist der mit Abstand älteste und am vollständigsten überlieferte fossile Ameisenbär. Zugleich ist es der einzige Nachweis eines Ameisenbären außerhalb der Neotropis. Die Fossilfunde der Vermilingua sind im übrigen auf ihr heutiges süd- und mittelamerikanisches Verbreitungsgebiet beschränkt und reichen dort nur bis zum Unter-Miozän (Santa Cruz-Formation Argentiniens) zurück. Diese neuweltlichen Fossilfunde sind sehr fragmentarisch und selten.

Das Typus-Skelett von *E. joresi* aus der Grube Messel bei Darmstadt weist außerordentlich weitreichende Übereinstimmungen mit den rezenten Gattungen *Myrmecophaga* und insbesondere *Tamandua* auf. Signifikante gemeinsame Sonderanpassungen liegen beispielsweise im Bau von Schädel und Unterkiefer, Vorderextremität und Becken. Daneben gibt es nur wenige Unterschiede, die auf Primitivausprägung von Merkmalen bei *Eurotamandua* beruhen. Als Beispiele sind der geschlossene Jochbogen und die vollständige Clavicula zu nennen. Lediglich der Bau der Gehörregion fällt anscheinend deutlicher aus dem Rahmen übereinstimmender biologischer Anpassungen von rezenten und fossilen Taxa. Aus einer konventionellen Röntgen-Schichtaufnahme (Storch 1981) wurde auf einen halbringförmigen, schmalen Anulus tympanicus geschlossen. *Tamandua* und *Myrmecophaga* besitzen hingegen eine sehr komplex aufgebaute Bulla tympanica mit tympanalen Nebenhöhlen. Diese Diskrepanz fordert zu einer Neuuntersuchung auf. Weiterhin soll geprüft werden, ob bei *Eurotamandua* wie bei den rezenten Ameisenbären ein extrem

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verlängerter knöcherner Gaumen ausgebildet ist, der die Choanen bis in die Nähe des Foramen magnum zurückversetzt. Diese Konfiguration stellt eine auffällige Autapomorphie der Vermilingua dar. Frühere Röntgenmethoden ließen keine Aussagen über die Morphologie der Schädelbasis zu. Über die deskriptiven Sachverhalte hinaus soll auf die mögliche Funktion und biologische Bedeutung der Apomorphien von Schädelbasis und Gehörregion eingegangen werden.

Die Präparationsmethoden von Wirbeltierfossilien aus der Grube Messel können für die wissenschaftliche Auswertung Probleme mit sich bringen. Die Skelette werden im Verband auf eine Kunstharz-Trägerplatte transferiert, wodurch bestimmte Aufsichten auf das Fossil – z. B. auf die Schädelbasis von *Eurotamandua* – nicht mehr möglich sind. Einen Ausweg bieten Röntgenverfahren. Mit Unterstützung der Werner-von-Siemens-Stiftung und der Deutschen Forschungsgesellschaft konnte am Forschungsinstitut Senckenberg eine digitale Radiographie aufgebaut werden (Habersetzer und Schaal 1990). Sie ermöglicht die Darstellung von Detailstrukturen, wie sie mit konventionellen Röntgenbildern nicht zu erreichen ist.

Material und Methode

Untersuchungsmaterial

Für die radiologische Neuuntersuchung stellte Herr Dr. G. Jores, Darmstadt, den in seinem Besitz befindlichen Holotypus von *Eurotamandua joresi* Storch, 1981 aus der Grube Messel zur Verfügung. Das rezente osteologische Material stammt aus den Sammlungen des Forschungsinstituts Senckenberg, Frankfurt am Main (SMF). Folgende Arten (in Klammern Anzahl der Schädel) wurden herangezogen: *Cyclopes didactylus* (Linnaeus, 1758) (6); *Myrmecophaga tridactyla* Linnaeus, 1758 (4); *Tamandua mexicana* (Saussure, 1860) (1); *T. tetradactyla* (Linnaeus, 1758) (8); *Manis gigantea* Illiger, 1815 (1); *M. javanica* Desmarest, 1822 (3); *M. pentadactyla* Linnaeus, 1758 (1); *M. temminckii* Smuts, 1832 (1); *M. tetradactyla* Linnaeus, 1766 (1) und *M. tricuspis* Rafinesque, 1821 (1). Den Abbildungen liegen die folgenden Exemplare zugrunde: Abb. 1: SMF 20 048; Abb. 2: SMF 18 190; Abb. 3: Coll. JORES, Darmstadt; Abb. 4: SMF 33 554; Abb. 5: SMF 15 424; Abb. 6: SMF 59 390.

Röntgentechniken

Die Übersichtsaufnahmen (Abb. 3–6a) wurden mit einem Siemens Nanodor 2 auf einem 40-4-HD-Bildverstärker erstellt. Die Röntgenbilder wurden über das Transicon-Verfahren nachbearbeitet. Die Detail-Radiographien (Abb. 4b, 6b) wurden auf Materialprüffilm (DuPont NDT 35) angefertigt und mit photographischen Masken nachbearbeitet.

Frühere Röntgenuntersuchungen an *Eurotamandua* wurden in der Ebene der Kunstharz-Trägerplatte des Fossils ausgeführt (Storch 1981). Bei den Neuuntersuchungen haben wir dagegen die Fossilplatte in Serienaufnahmen um bis zu 60° in der cranio-caudalen Achse verkippt. Durch „Freiprojektion" wurde erkannt, daß die Bulla tympanica und die benachbarten Strukturen nur auf der rechten Schädelseite erhalten sind. Der Aufnahmewinkel in Abb. 3a–b lag bei 35°, bedingt durch die ursprüngliche schräge Einbettung des Schädels im Gestein. Durch stärkeres oder schwächeres Verkippen unter Röntgendurchleuchtung war ein Mitdrehen von Schädelbasis und knöchernem Gaumen bei unveränderter Lagebeziehung zur Ohrregion zu beobachten. Demgegenüber veränderte die hintere Jochbogenwurzel, die vom Schädel seitlich etwas absteht, ihre Lage perspektivisch. Entsprechend der Schädelerhaltung von *Eurotamandua* wurden von den rezenten Arten Schädelhälften in Lateralansicht geröntgt.

Ergebnisse und Diskussion

Schädelbasis und Gehörregion rezenter Ameisenbären

Zur Osteologie von Temporal- und Pterygo-Alisphenoid-Region:

Ameisenbären zeichnen sich durch bemerkenswerte Sonderanpassungen des Kauapparates, der Vorderextremitäten und des Verdauungstraktes aus, die in Verbindung mit der hochspezialisierten insektivoren Ernährungsweise stehen – dem Fressen von vorzugsweise Ameisen und Termiten. Aber auch das Basicranium und die Temporalregion haben im

Zusammenhang mit der Myrmecophagie Umgestaltungen erfahren, wie sie einmalig unter Säugetieren sind. Schädelanatomisch gleichen sich die beiden Gattungen *Myrmecophaga* Linnaeus, 1758 und *Tamandua* Gray, 1825 weitgehend, und die im folgenden für *Tamandua* dargelegten Verhältnisse können grundsätzlich für *Myrmecophaga* übernommen werden. Dagegen weicht die dritte rezente Gattung, *Cyclopes* Gray, 1821, in eingen Eigenheiten ab.

Die folgenden Beschreibungen basieren auf eigenem Material (Forschungsinstitut Senckenberg) und den Angaben von van Kampen (1905) und vor allem von Guth (1961).

Tamandua

Der knöcherne Gaumen verlängert sich derart nach hinten, daß die Choanen im Hinterhauptbereich kurz vor dem Foramen magnum liegen. Eine vergleichbare Konfiguration tritt bei keinem anderen terrestrischen Eutherier auf, lediglich Wale zeigen geringgradig eine ähnliche Entwicklung. Der harte Gaumen wird von den langen, kräftig entfalteten Palatina und Pterygoidea gebildet, deren horizontale Gaumenfortsätze sich jeweils in der Medianlinie zusammenschließen. Die Pterygoidea begrenzen somit die hintere ventrale Wand des sehr langen Nasopharynx und beteiligen sich an der Umfassung der Choanen (Abb. 2).

Die Verlängerung des harten Gaumens und die Rückverlagerung der Choanen verursachen beträchtliche Abänderungen in der Gehörregion, insbesondere in den Lagebeziehungen bestimmter Schädelöffnungen und in der Zusammensetzung der knöchernen Bulla. So wird beispielsweise die Tubenöffnung, die bei Säugern gewöhnlich in der vorderen Umgrenzung der Paukenhöhle liegt, in deren hinteren Bereich zurückversetzt. Dort wird das Ostium tubae von Ectotympanicum, Processus tympanicus des Basioccipitale und Pterygoid eingefaßt (Abb. 2) (Zuckerkandl 1904; Denker 1905).

Der Aufbau der Bulla tympanica und die Lage und Ausdehnung tympanaler Nebenhöhlen sind für *Tamandua* und *Myrmecophaga* in hohem Maße kennzeichnend und in vergleichbarer Form von keinen anderen Säugern bekannt. Die Anzahl der an der Begrenzung der geräumigen Paukenhöhle beteiligten Schädelknochen erreicht hier ein Maximum. Von denjenigen Elementen, die sich überhaupt an der Bulla beteiligen können (Petrosum, Ectotympanicum, Squamosum, Alisphenoid, Entotympanicum, Basisphenoid, Basioccipitale, Pterygoid, Exoccipitale, Processus Folii des Malleus = Goniale, Tympanohyale; van Kampen 1905), bilden alleine 9 den knöchernen Mittelohr-Komplex der beiden Ameisenbären-Gattungen.

Das geschlossen-ringförmige Ectotympanicum ist eng mit Petrosum und Squamosum verschmolzen. Es verbreitert sich ventral sehr stark und bildet nach außen einen Recessus meatus und nach innen die untere Wand des Cavum tympani. Der Trommelfellring ist stark geneigt. Ein stark reduziertes, caudales Entotympanicum ist bei *Myrmecophaga* und *Tamandua* nach Guth (1961) vorhanden: Es beteiligt sich als kleine Knochenlamelle an der Bildung der Rückwand des Cavum tympani. Es ist zwischen Petrosum, Exoccipitale und Tympanicum eingeschoben und liegt in der Vorderwand der Grube, die in das Foramen jugulare führt (Abb. 2). Einschränkend ist allerdings festzuhalten, daß bei Ameisenbären – im Unterschied etwa zu Dasypodiden (Reinbach 1952) – kein positiver embryologischer Beleg für ein Entotympanicum vorliegt. An Stelle des rückgebildeten Entotympanicums beteiligt sich der Processus tympanicus des Basioccipitale an der medialen Wand der Paukenhöhle (Abb. 1b). Dieser Knochenfortsatz ist zum Cavum tympani hin etwas ausgehöhlt und bildet auf diese Weise eine kleine tympanale Nebenhöhle. Vervollständigt wird die Innenwand und der medioventrale Teil der Bulla nach vorn von einer annähernd vertikalen Lamelle des Ptergyoids, auf die sich auch die eben genannte Nebenhöhle ausdehnt (Abb. 1b). Nach oben setzt sich die Paukenhöhle in Form des tiefen Recessus epitympanicus für Hammer und Amboß in das Squamosum fort, und ein kleiner

Sinus im Sqamosum erweitert noch den epitympanalen Raum. Die obligate Beteiligung des Petrosum an der Begrenzung des Mittelohrraumes erstreckt sich auf den dorsomedialen (Promontorium) und dorsocaudalen (Pars mastoidea) Bereich. Die Wand der Pars mastoidea an der Schädelaußenseite ist bei *Tamandua* relativ dünn und stellt den Boden der weiten, tiefen Fossa subarcuata dar (Abb. 1a–b). Bei *Myrmecophaga* ist diese Fossa seichter. Schließlich bilden noch Tympanohyale und Processus Folii weitere, wenn auch unbedeutende Bestandteile der Bulla ossea. Ersteres liegt, durch Suturen kaum abgrenzbar, zwischen Ectotympanicum, Exoccipitale und Pars mastoidea des Perioticums. Der Processus Folii ist eng mit dem Ectotympanicum verschmolzen, an dessen Vorderrand er einen kleinen Knochenvorsprung ausbildet.

Eine sehr auffällige Autapomorphie der Gattungen *Tamandua* und *Myrmecophaga* ist eine große Nebenhöhle, die vor dem Cavum tympani gelegen ist und mit ihm weit kommuniziert (Abb. 1a–b). Schon früh wurde erkannt (z. B. Hyrtl 1845; Flower 1885), daß es sich hierbei um einen hypotympanalen Sinus handelt. Dennoch hat sich in Lehrbüchern vielfach die Ansicht gehalten, daß diese Höhle vom Nasen-Rachen-Raum ausgeht und keinerlei Verbindung zum Mittelohr hat (z. B. Grassé 1955; Moore 1981; Stadtmüller 1936; Starck 1979; Weber 1928).

Die akzessorische Bulla tympanica, welche die Nebenhöhle umschließt, wölbt sich am harten Gaumen vor dem Ectotympanicum als flache Beule vor (Abb. 2). Sie wird von Pterygoid und Alisphenoid gebildet. Es ist schwierig, die Anteile beider Knochen auseinanderzuhalten, da sie sehr früh miteinander verschmelzen. Im Anschluß an Guth (1961) bezeichnen wir diesen Komplex daher als Pterygo-Alisphenoid (Abb. 1b). Es kann aber festgehalten werden, daß das Pterygoid die medioventrale Wand und das Alisphenoid die Dorsalwand bilden, und daß beide Knochen sich an der Außen- und Innenwand beteiligen. An juvenilen Schädeln von *Tamandua tetradactyla* (Senckenberg-Museum, SMF 11449, 12947) verläuft in Ventralansicht die Naht zwischen Alisphenoid und Pterygoid über den rostrolateralen Bereich der akzessorischen Bulla. Das Alisphenoid schließt dementsprechend das Foramen ovale vollständig ein (die Naht zwischen For. ovale und Squamosum in Abb. 2 entsteht bei der Vereinigung von zwei lateralen Alisphenoid-Schenkeln). Die tympanale Nebenhöhle ist voluminöser als das Cavum tympani (bei *Myrmecophaga* ist dieser Unterschied beträchtlich). Die beiden Räume sind durch eine kräftige, hohe Crista des Pterygo-Alisphenoids (Abb. 1b) und eine häutige Membran teilweise voneinander getrennt. Sie kommunizieren über eine weite Perforation in dieser Membran (van Kampen 1905; eignes Material).

Ein weiterer großer Sinus liegt bei *Tamandua* im knöchernen Gaumen jeweils vor der akzessorischen Bulla (Abb. 1b). Er dehnt sich hauptsächlich im Palatinum aus, erstreckt sich aber auch auf den vorderen Teil des Alisphenoids. Dieser pneumatische Raum steht in keiner Verbindung mit dem Mittelohr und seinen Nebenhöhlen. Er fehlt bei *Myrmecophaga*.

Cyclopes

Auch beim Zwergameisenbären, *Cyclopes didactylus,* erstrecken sich die Pterygoidea weit nach hinten bis vor das Foramen magnum, und sie bilden horizontale Gaumenplatten aus. Im Unterschied zu *Tamandua* und *Myrmecophaga* berühren sich die Pterygoidea und das caudale Drittel der Palatina nicht in der Medianlinie, sondern lassen einen Spalt zwischen sich frei. Dieser Spalt wird durch eine derbe bindegewebige Membran verschlossen (Parker 1886), so daß auch hier ein sehr langer Nasopharynx und sehr weit rückverlagerte Choanen vorliegen. Der vollständig knöchern geschlossene Gaumen von *Tamandua* und *Myrmecophaga* stellt gegenüber den Verhältnissen bei *Cyclopes* sicherlich den abgeleiteten Zustand dar. Funktionell wird aber – besonders auch im Hinblick auf die wesentlich geringere Schädelgröße von *Cyclopes* – kein gravierender Unterschied zwischen beiden Verschlußmodi des Gaumens bestehen.

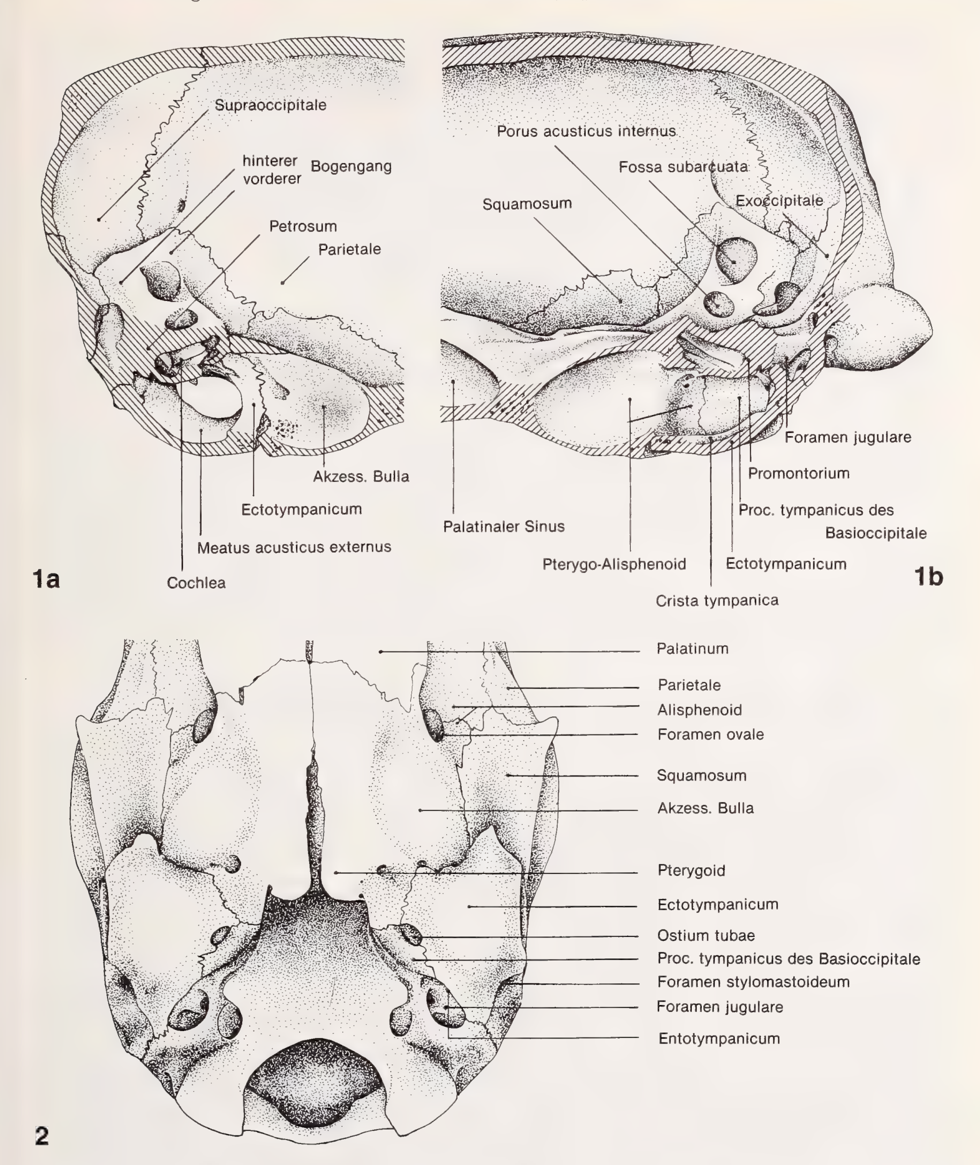


Abb. 1–2. Schädel von *Tamandua tetradactyla, 1a–b:* Parasagittaler Schnitt durch die Gehörregion der linken Seite. a = Aufsicht von medial, b = Aufsicht von lateral.
2: Schädelbasis in Ansicht von ventral

In der Gehörregion von *Cyclopes* fällt vor allem auf, daß eine akzessorische Bulla tympanica fehlt. Weder Pterygoid noch Alisphenoid weisen auch nur im Ansatz eine Pneumatisierung für tympanale Nebenhöhlen auf (Abb. 5). Der Erwerb einer akzessorischen Bulla bei *Tamandua* und *Myrmecophaga* wird ebenfalls als abgeleiteter Zustand gewertet.

Das Cavum tympani ist sehr geräumig. Das ringförmige Ectotympanicum ist unten und hinten stark verbreitert. Ein schmaler rostrodorsaler Abschnitt des Ectotympanicums

überbrückt eine längliche Konkavität in der Außenseite des Squamosums, die nach hinten in den Recessus epitympanicus einmündet. Das Basioccipitale ist von der Wand der Paukenhöhle ausgeschlossen. Petrosum, Tympanohyale und – nach Guth (1961) – ein kleines Entotympanicum bilden die Rückwand der Bulla, und Pterygoid, Alisphenoid, Squamosum und Ectotympanicum stellen ihre Vorderwand. Nach ventral erfolgt der Abschluß innen durch das Pterygoid und außen durch das Ectotympanicum. Die Fossa subarcuata im Petrosum ist wie bei *Tamandua* weit und sehr tief.

Radiologische Darstellung

Die beiden auffälligsten apomorphen Merkmale von Schädelbasis und Gehörregion der Ameisenbären ergeben im Röntgenbild eine sehr kennzeichnende Konfiguration. Der extrem lange, unten von horizontalen Gaumenplatten begrenzte Nasopharynx zeichnet sich dorsal und ventral als schnurgerade Kontur ab (Abb. 4a, 5). Hierbei handelt es sich um eine Autapomorphie der Unterordnung Vermilingua. Die Gehörregion von *Tamandua* (Abb. 4a) zeigt drei aneinandergrenzende, ungefähr gleichgroße Hohlräume, die mehr oder weniger kreisförmig umschrieben sind. Es sind von vorn nach hinten die akzessorische Bulla tympanica, die Paukenhöhle und – dorsocaudal an das Cavum tympani anschließend – die Fossa subarcuata im Perioticum. Die Bulla tympanica liegt weit hinten an der Schädelbasis. Die rostrale tympanale Nebenhöhle stellt eine Autapomorphie der Familie Myrmecophagidae dar; bei *Cyclopes* (Familie Cyclothuridae) ist sie auch andeutungsweise nicht vorhanden (Abb. 5).

Zur Funktion und biologischen Rolle des verlängerten Gaumens und der akzessorischen Bulla tympanica

Die extreme Verlängerung des knöchernen Gaumens bei den Ameisenbären steht in Verbindung mit der myrmecophagen Ernährungsweise. (Eine derartige Verlängerung fehlt bei den ebenfalls myrmecophagen *Orycteropus, Proteles* und *Myrmecobius*. Sie besitzen Zähne und ihre Kaumuskeln und Kiefergelenke sind nicht wie bei Ameisenbären rückgebildet; sie sind daher in der Lage, die Insektennahrung im Mund zu manipulieren. Rückverlagerte Choanen kommen sonst bei Wirbeltieren mit aquatiler Lebensweise wie Walen vor). Mächtige Speicheldrüsen feuchten die wurmförmige, weit ausstreckbare Zunge an, und mit ihrer Hilfe werden große Mengen von Ameisen und Termiten und gelegentlich auch Larven anderer Insekten aufgenommen. Die völlige Zahnlosigkeit, die dünnen spangenförmigen Unterkiefer und die nur locker dem Schädel angelagerten Gelenkköpfchen der Unterkiefer verhindern wirkungsvolles Kauen. Die Nahrung wird nicht in Form von diskreten Bissen in die Mundhöhle aufgenommen oder zwischen den Kiefern entsprechend manipuliert, sondern sie besteht aus einer großen Zahl von kleinen Partikeln, die über die ganze Zunge verteilt sind. Der verlängerte Gaumen schließt die enge Röhre, in der die Zunge gleitet, nach oben ab, und er stellt ein solides Widerlager dar für eine feste, dicke Wangenfalte, die ihm beiderseits angepreßt ist. Diese Einrichtung unterstützt den Nahrungstransport zum Schlund, da nur Insekten auf dem hinteren Zungenabschnitt beim Zurückziehen in den Schluckbereich gelangen. Nach Kühlhorn (1939) pressen die Kiefer die Wangenfalten beim Herausstrecken der Zunge weit nach median, so daß Insekten von der vorderen Zunge von Wangenpapillen abgekämmt werden können. Beim Einziehen kämmen dann ihrerseits Borsten des hinteren Zungenabschnitts diese Insekten ab und befördern sie zu den Schluckeinrichtungen.

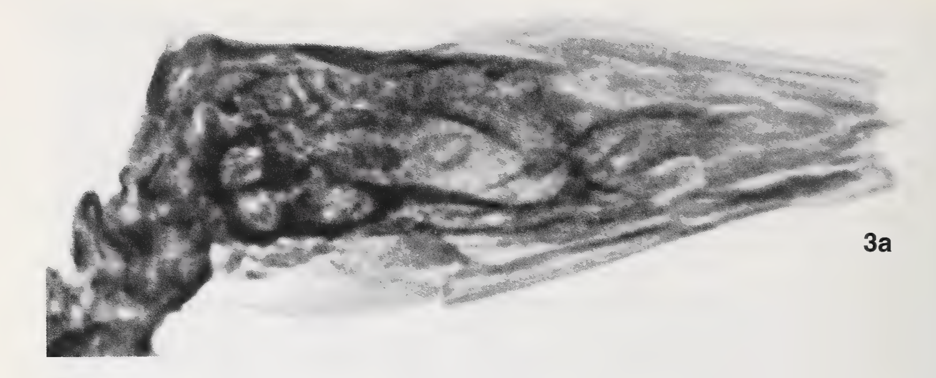
Die aufgenommenen Insekten sind gewöhnlich mobil und vielfach sehr aggressiv. Es muß daher erreicht werden, daß die Nasenhöhlen von innen her vor eindringenden Ameisen und Termiten geschützt werden. *Tamandua* und *Myrmecophaga* fressen durchaus auch solche Arten, die für ihre sehr aggressive Nestverteidigung durch Beißen, Stechen

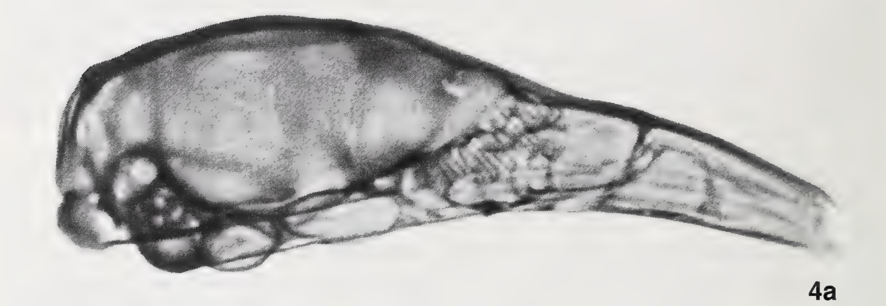
oder Absonderung chemischer Mittel bekannt sind (Redford 1987). Der verlängerte harte Gaumen, der die Choanen bis in die Occipitalregin verlagert, stellt eine weitreichende, wirkungsvolle Trennwand hierfür dar.

Die akzessorische Bulla von *Tamandua* und *Myrmecophaga* bewirkt eine erhebliche Vergrößerung des Tympanalraumes. Für die Schallübertragung ergibt sich hieraus eine geringere Dämpfung für tieffrequente Schallwellen und damit eine Empfindlichkeitssteigerung für tiefe Töne. Möglicherweise wirkt die akzessorische Bulla sogar als Helmholtz-Resonator, und es kommt zu einer Verstärkung in einem engen Bereich tiefer Frequenzen, der ökologisch wichtige Schallereignisse umfaßt. Für einen Resonator spricht die relativ abgeschlossene Form der tympanalen Nebenhöhle mittels eines Knochenkammes und einer perforierten Membran. Bei terrestrischen, nicht subterran lebenden Säugern wird die Mittelohr-Vergrößerung zur Sensitivitätssteigerung für tiefe Frequenzen entweder im Kontext mit einer Feindvermeidung und/oder mit offenen Lebensräumen wie Wüsten oder Halbwüsten gesehen (z. B. Webster 1966; Novacek 1977; Fleischer 1978). Diese biologischen Rollen sind jedoch schwerlich auf *Tamandua* und *Myrmecophaga* zu beziehen. Die Tiere zeichnen sich durch sehr geringe Fluchtdistanzen und -geschwindigkeiten aus und verlassen sich gegenüber Feinden auf Drohen und blitzschnelles Zuschlagen mit den muskelbepackten und krallenbewehrten Vorderextremitäten (Krieg und Rahm 1961). Tieffrequente Schallwellen haben für Wüstentiere den Vorteil geringerer atmosphärischer Abschwächung. Ihre größere Reichweite ist sehr wichtig für soziale Kontakte bei Säugern wie den Ctenodactyliden, die verstreut in der Weite von Wüsten leben. Einer solchen Situation werden weder die Lebensräume noch das bekannte Sozialverhalten der Ameisenbären gerecht.

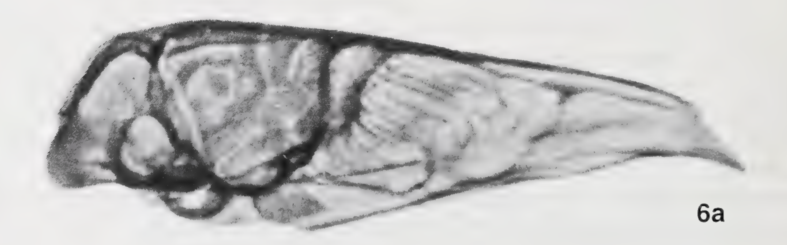
Wir vermuten hingegen, daß die akustische Spezialisation der beiden Ameisenbären-Gattungen in Verbindung mit dem Nahrungserwerb steht. Extreme Sonderanpassungen der gesamten Vorderextremität, von denen einige Autapomorphien der Vermilingua darstellen, dienen dem Aufbrechen von oft betonharten Termitenbauten und ameisenbefallenem Holz (Storch 1981; Taylor 1985). Wir gehen davon aus, daß beim Anschlagen der festen Insektennester eine Art Perkussion erfolgt. Bei der Perkussion von Hohlräumen wirken hochfrequente, an der Oberfläche entstehende Geräusche störend, während die Lage und die Ausdehnung eines unter der Oberfläche gelegenen Hohlraumes durch Intensität und Dauer (d. h. die Dämpfung der Eigenresonanz) tieffrequenten Schalls mitgeteilt wird. Im Sinne eines gezielten und schnellen Aufbrechens der Bauten erscheint uns die Funktion der akzessorischen Bulla tympanica als akustische Anpassung an den Nahrungserwerb sehr naheliegend. *Cyclopes* besitzt keine derartige tympanale Nebenhöhle. Dieser Unterschied mag damit zusammenhängen, daß *Cyclopes* sich ausschließlich von Ameisen ernährt und keine harten Termitenbauten aufbricht (Montgomery 1985; Redford 1987; Taylor 1985).

Etwas ungewöhnlich mag die Lage der akzessorischen Bulla erscheinen. Das Mittelohr muß physiologische Anforderungen im Rahmen der artspezifischen räumlichen und morphologischen Bedingungen am Schädel erfüllen (Fleischer 1978; Maier 1990). Eine voluminöse Bulla tympanica würde sich nicht in das Konstruktionsprinzip des glattröhrenförmigen Schädels von *Tamandua* und *Myrmecophaga* einfügen. Die Ausbildung von Nebenhöhlen in der Pars mastoidea des Perioticums, die bei Eutheria eine verbreitete Lösung darstellt, scheidet aus Platzgründen aus, denn das Cavum tympani ist schon sehr weit hinten am Schädel gelegen (Abb. 1a–b, 4a). Dafür stellt die Pterygo-Alisphenoid-Region am verlängerten harten Gaumen Material für einen hypotympanalen Sinus rostral von der Paukenhöhle zur Verfügung.


3a


4a


5


6a

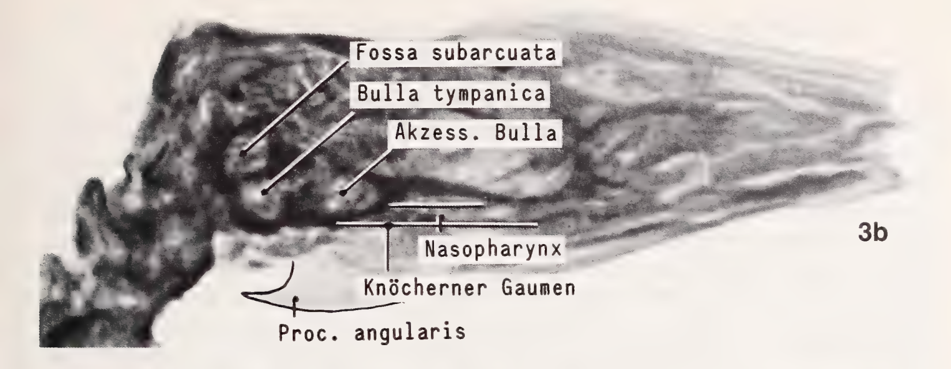


Abb. 3–6. Röntgenaufnahmen von Ameisenbären- und Schuppentier-Schädeln von lateral. Alle Schädel sind in der Mediosagittalebene halbiert. *3a–b: Eurotamandua joresi,* Holotypus aus dem Mitteleozän der Grube Messel bei Darmstadt. Der Facialschädel vor der Orbita ist stark zerdrückt und in der Horizontalebene ausgebreitet. *4a–b: Tamandua tetradactyla. a* = Übersichtsaufnahme, *b* = Detailradiographie der Gehörregion. *5: Cyclopes didactylus.* Übersichtsaufnahme. *6a–b: Manis javanica. a* = Übersichtsaufnahme, *b* = Detailradiographie der Gehörregion

Verlängerter harter Gaumen und akzessorische Bulla tympanica bei *Eurotamandua joresi* aus Messel

Der Myrmecophagide *Eurotamandua joresi* wurde an Hand eines fast vollständigen, sehr plastisch erhaltenen Skelettes aus dem unteren Mittel-Eozän (= unteres Geiseltalium, Paleogene Mammal Unit MP 11) der Grube Messel bei Darmstadt beschrieben (Storch 1981). Hinzu kamen später leicht fragmentierte Einzelknochen – Ulna und Radius – aus der etwa gleichaltrigen Unterkohle des Geiseltals bei Halle (Storch und Haubold 1989). Dieses Fossilmaterial zeigt zum einen die autapomorphen Merkmale der Xenarthra: Xenarthrale Wirbelverbindungen im hinteren Rumpfbereich und Synsacrum durch Synostose zwischen Ischium und Pseudosacralwirbeln. Ebenso deutlich sind auch bereits Autapomorphien der Familie Myrmecophagidae ausgeprägt: Spezialanpassungen von Metacarpale 3 und Mittelfinger sowie von Entepicondylus und Deltopectoralgebiet des Humerus (Einzelheiten siehe bei Storch 1981; Storch und Haubold 1989). Außerordentlich weitreichend ist die osteologische Übereinstimmung mit der rezenten Gattung *Tamandua*, und demtentsprechend groß sind Unterschiede zu *Cyclopes* (Familie Cyclothuridae).

Harter Gaumen, Nasopharynx und Schädelbasis von *Eurotamandua* (Abb. 3a) zeigen das gleiche Bild, das für rezente Myrmecophagiden so außerordentlich kennzeichnend ist (Abb. 4a). Der knöcherne Gaumen bildet als auffällig geradlinige Kontur die ventrale Begrenzung des Schädels bis weit in den Bereich der akzessorischen Bulla nach hinten. Weiter dorsal und parallel dazu liegt die Schädelbasis, und beide Linien schließen den sehr langen Nasopharynx ein (Abb. 3b). Die verlängerten Pterygoidea von *Eurotamandua* sind wie bei den heutigen Vermilingua mit horizontalen Gaumenfortsätzen ausgestattet, und somit sind die Choanen in den occipitalen Bereich rückverlagert. In den Fällen, in denen sich die Pterygoidea nur mit vertikalen Platten caudad verlängern, ergibt sich eine abweichende Konfiguration im Röntgenbild (Abb. 6a). *Eurotamandua* besitzt keinen paranasalen Sinus im Palatinum wie *Tamandua* (Abb. 4a) und gleicht hierin *Myrmecophaga*.

Der Vergleich der Gehörregion von *Eurotamandua joresi (Abb. 3a) und Tamandua tetradactyla* (Abb. 4a) läßt klar erkennen, daß sowohl die Größenverhältnisse als auch die Lagebeziehungen von Bulla tympanica, akzessorischer Bulla und Bogengangsapparat (erkenntlich an dem durch die Fossa arcuata umschriebenen Raum) sehr ähnlich sind. Der gesamte Komplex liegt bei beiden Arten weit aboral am Schädel. Es ist zu vermuten, daß sich die Cochlea bei *Eurotamandua* ebenso wie bei *Tamandua* deutlich über der Schädelbasis befindet und im Unterschied zu *Cyclopes* (Abb. 5) und *Manis* (Abb. 6a) nach ventral einem großen Tympanalraum Platz gibt. Die Ausbildung der für Myrmecophagidae hochrangig autapomorphen akzessorischen Bulla bei *Eurotamandua* und deren Größen- und Lageübereinstimmung mit *Tamandua* läßt uns annehmen, daß sich auch der anatomische Aufbau der Gehörregion mit den Verhältnissen bei den rezenten Arten deckt. *Myrmecophaga* besitzt eine im Verhältnis zum Cavum tympani größere hypotympanale Nebenhöhle als *Eurotamandua* und *Tamandua*. Bei den Cyclothuridae (*Cyclopes*; Abb. 5) fehlt eine akzessorische Bulla.

Wir können also die früher vermutete halbringförmige Struktur eines offenen Ectotympanicums, wie sie sich im konventionellen Röntgentomogramm zeigte (Storch 1981), hier nicht bestätigen. Da seinerzeit die Röntgen-Schnittebenen parallel zur Oberfläche der Fossilträgerplatte gelegt waren, betrug die Orientierung zum Schädel ungefähr 35° ventrolateral. Dadurch sind eine Reihe von möglichen Anschnitten mit nur unvollständiger Erfassung einer geschlossenen Bulla tympanica denkbar.

Unterschiede zwischen *Eurotamandua* und Schuppentieren (Pholidota) an Schädelbasis und Gehörregion

Myrmecophage Säugetiere weisen eine große Anzahl konvergent entstandener Merkmale auf. So ist bei Myrmecophagiden, Pholidoten und Tachyglossiden in Verbindung mit dem langen Gaumen die Tubenöffnung in den caudalen Bereich des Cavum tympani gerückt. Innerhalb der Eutheria stellen sowohl die Xenarthra als auch die Pholidota offensichtlich sehr früh abgezweigte, in manchen Merkmalen außerordentlich primitive, persistierende Gruppen dar (Starck 1941). Dies erschwert die Suche nach apomorphen Kriterien und erklärt die große Divergenz heutiger Klassifikationen. *Eurotamandua* wurde – vor allem vor dem Hintergrund paläobiogeographischer Probleme – von Novacek (1982, 1990) und Rose (1984) als mögliches, vielleicht aberrantes Schuppentier und von McKenna (1987) als Palaeanodonte klassifiziert. (Zur vermeintlichen paläobiogeographischen Unvereinbarkeit eines Ameisenbären-Fundes in Europa siehe Storch 1986, 1990.) Daher soll hier auf die gravierenden, gruppenspezifischen Unterschiede von Schädelbasis und Gehörregion zwischen *Eurotamandua* (Abb. 3a) und *Manis* (Abb. 6a) hingewiesen werden. Zum abweichenden Bau der Ohrregion der Palaeanodonta (Familien Metacheiromyidae und Epoicotheriidae) kann auf die Arbeiten von Simpson (1931), Emry (1970) und Rose und Emry (1983) verwiesen werden.

Der harte Gaumen von *Manis* wird nach hinten von den Palatina begrenzt. Die Pterygoidea sind sehr lang und reichen mit vertikalen Platten beiderseits bis zum Ectotympanicum aborad. Sie bilden aber im Unterschied zu den Vermilingua keine horizontalen Gaumenplatten aus. Die Röntgenbilder veranschaulichen dies: Bei *Eurotamandua*, *Tamandua* und *Cyclopes* laufen Schädelbasis und harter Gaumen als geradlinige parallele Konturen bis zur Bulla tympanica bzw. zur akzessorischen Bulla nach hinten durch (Abb. 3a, 4a, 5), während bei *Manis* die untere gerade Kontur des harten Gaumens weit vorher abbricht und sich in Form des leicht dorsad geschwungenen, weniger dichten Ventralrandes der vertikalen Pterygoidlamelle bis zum Ectotympanicum fortsetzt (Abb. 6a).

Das Ectotympanicum von *Manis* hat die Form eines mehr oder weniger breiten, nach oben nicht ganz geschlossenen Ringes. Anders als bei den Vermilingua verwächst es nicht mit seiner Umgebung, um eine geräumige, komplex zusammengesetzte Bulla tympanica zu bilden (Abb. 6b). Auch für die unteroligozäne nordamerikanische Maniden-Gattung *Patriomanis* gibt es keinen Hinweis auf eine am Schädel befestigte Bulla (Emry 1970). Im Vergleich zu *Eurotamandua* und den rezenten Myrmecophagidae besitzt *Manis* einen sehr kleinen Hypotympanalraum. Dies kommt auch in der mehr ventralen Lage von Cochlea und Vestibularorgan – bezogen auf die Schädelbasis – bei *Manis* (Abb. 6b) gegenüber *Tamandua* (Abb. 4b) zum Ausdruck. *Eurotamandua* verhält sich hierin aufgrund der Lagebeziehungen von Bulla und Schädelbasis (Abb. 3a) wie *Tamandua*.

Maniden besitzen keine hypotympanalen Nebenhöhlen, dafür aber einen sehr ausgedehnten Sinus epitympanicus, wodurch sie sich auffällig von den Myrmecophagiden unterscheiden. Das Cavum tympani von *Manis* wird von Petrosum, Squamosum und Ectotympanicum begrenzt. (Van Kampen [1905] sprach ein sehr kleines Knöchelchen zwischen Ectotympanicum und Petrosum bei *M. tricuspis* und ein entsprechendes, kräftigeres Knochenelement bei *M. gigantea* als wahrscheinliches Entotympanicum an. Bei 5 weiteren *Manis*-Arten fand er keine Spur eines Entotympanicum, und auch Jollie [1968] bezweifelt dessen Existenz bei *M. javanica*.) Das Cavum tympani ist membranös in zwei kommunizierende Abschnitte unterteilt, einen unteren für Trommelfell, Hammergriff und Ostium tubae und einen oberen für die Gehörknöchelchen, den Musculus stapedius und die Paukenfenster (Eschweiler 1899). Die Paukenhöhle setzt sich nach dorsocaudal über ein weiteres Foramen pneumaticum in einen großen epitympanalen Sinus fort, der den hinteren Teil des Squamosums aufbläht (Abb. 6b). Im Röntgenbild ergeben sich damit

unterschiedliche Konfigurationen: Die dorsocaudale Ringstruktur in der Gehörregion umschreibt bei den Ameisenbären (Abb. 3a, 4a, 5) die Fossa subarcuata. Die entsprechende Struktur von *Manis* (Abb. 6a–b) grenzt die epitympanale Nebenhöhle ab; sie ist größer und gegenüber dem Ectotympanicum viel weiter aborad ausgedehnt. Insbesondere fehlt den Ameisenbären auch das markante Tentorium osseum zwischen Fossa cerebralis und cerebellaris, das sich bei *Manis* in bezeichnender Weise in die rostrale Kontur des Sinus epitympanicus fortsetzt (Abb. 6a).

Eurotamandua weist also weder am harten Gaumen noch in der Gehörregion Merkmale auf, die eine Zuordnung zu den Pholidoten rechtfertigen oder überhaupt erst nahelegen würden.

Phylogenetische Schlußfolgerungen

Es gibt eine Reihe von gewichtigen Argumenten, die traditonelle Zweiteilung der Xenarthra in Pilosa Flower, 1883 (Ameisenbären + Boden- und Baumfaultiere) und Cingulata, Illiger 1811 (Gürteltiere i. w. S.) aufzugeben. Die Vermilingua nehmen innerhalb der Xenarthra eine isolierte Position ein und müssen schon sehr früh von einer gemeinsamen Wurzel abgezweigt sein. Diese Sonderstellung geht aus Untersuchungen so unterschiedlicher Merkmalskomplexe hervor wie beispielsweise: Verlauf der Arteria carotis interna (Bugge 1979), Osteologie der Temporalregion (Guth 1961), Fußbau, Ernährungssystem (Hoffstetter 1954, 1982), weiblicher Reproduktionstrakt (Novacek und Wyss 1986), Albumin-Immunologie (Sarich 1985).

Aus paläontologischer Sicht untermauern frühere (Storch 1981; Storch und Haubold 1989) und die hier vorgestellten Befunde an *Eurotamandua* die Annahmen einer sehr frühen Radiation der Xenarthra und eines entsprechend langen Eigenweges der Vermilingua. Der heutige Anpassungstyp *Tamandua* kann praktisch unverändert zu der 50 Millionen Jahre alten Gattung *Eurotamandua* zurückverfolgt werden. Die ältesten Nachweise unbestrittener Xenarthra stammen aus dem jüngeren Paläozän Südamerikas. Diese Funde sind eindeutig auf Gürteltiere – wahrscheinlich der dasypodiden und glyptodontiden Zweige (Cifelli 1983; Engelmann 1985) – zu beziehen. Es sind keine Fossilien bekannt, die zwischen den drei klar differenzierten Unterordnungen der Ameisenbären, Gürteltiere und Faultiere vermitteln. All dies legt es nahe, daß die frühesten Fossilnachweise wesentlich jünger sind als der Ursprung der betreffenden Gruppe, und daß die stammesgeschichtliche Aufspaltung der Xenarthra tief in der Kreidezeit erfolgt ist.

Die Bedeutung von *Eurotamandua* für die stammesgeschichtliche Rekonstruktion der Vermilingua reicht noch weiter. *Eurotamandua, Tamandua* und *Myrmecophaga* unterscheiden sich durch gemeinsame Sonderanpassungen der Hand und des Ellbogengelenks von *Cyclopes* (Storch 1981; Storch und Haubold 1989). Die vorliegende Untersuchung der Gehörregion hat ergeben, daß auch hier gavierende Unterschiede bestehen. *Eurotamandua, Tamandua* und *Myrmecophaga* besitzen in der akzessorischen Bulla tympanica eine sehr bemerkenswerte Synapomorphie. *Cyclopes* ist deutlich primitiver, denn hypotympanale rostrale Nebenhöhlen fehlen auch ansatzweise. Eine sekundär erfolgte Rückbildung einer morphologisch so komplexen Struktur, die im funktionellen Kontext des Hörens steht, schließen wir aus. Auch die *Cyclopes* nahverwandte Gattung *Palaeomyrmidon* aus dem Pliozän Argentiniens zeigt offensichtlich keine rostrale Erweiterung des Cavum tympani. Es ist zu folgern, daß die basale Dichotomie innerhalb der Vermilingua dem Auftreten von *Eurotamandua* im unteren Mittel-Eozän weit vorausgegangen ist und noch in der Kreide anzusetzen ist. Unsere Ansichten über das hohe erdgeschichtliche Alter der Vermilingua und ihrer beiden stammesgeschichtlichen Linien decken sich mit der Stammbaum-Darstellung bei Thenius (1988). Wir halten die Unterschiede zwischen *Cyclopes* und der Gruppe *Eurotamandua – Tamandua – Myrmecophaga* für so signifikant und gewichtig, daß wir sie wie Hirschfeld (1976) als Familien Cyclothuridae (= Cyclopedidae) und Myrmecophagidae trennen (die Abgrenzung in Form ranghöherer Taxa ist

durchaus auch zu erwägen). *Eurotamandua* belegt die Familie Myrmecophagidae mit ihren entscheidenden, bereits voll ausdifferenzierten Autapomorphien.

Klassifikation der Vermilingua

Die Validität der neogenen südamerikanischen Gattungen ist zum Teil fraglich. Hirschfeld (1976) bewertet *Promyrmephagus* als ein Synonym von *Protamandua* und *Nunezia* als Synonym von *Myrmecophaga*. Die neogenen Gattungen und Arten sind nur schwer miteinander vergleichbar, da sie in der Regel nach unterschiedlichen Skelettelementen beschrieben wurden (vgl. Hirschfeld 1976; Storch 1981).

Ordnung Xenarthra Cope, 1889
- Unterordnung Vermilingua Illiger, 1811
  - Familie Myrmecophagidae Gray, 1825
    - *Myrmecophaga* Linnaeus, 1758. Rezent, Pleistozän; Süd- und Mittelamerika (= *Nunezia* Kraglievich, 1934. Pliozän; Argentinien)
    - *Tamandua* Gray, 1825. Rezent, Pleistozän; Süd- und Mittelamerika
    - *Protamandua* Ameghino, 1904. Miozän; Argentinien (= *Promyrmephagus* Ameghino, 1904. Miozän; Argentinien)
    - *Neotamandua* Rovereto, 1914. Pliozän, Miozän; Argentinien, Kolumbien
    - *Eurotamandua* Storch, 1981. Eozän; Deutschland
  - Familie Cyclothuridae Gill, 1872 (ex Cyclothurinae Gill, 1872; Cyclopedidae Hirschfeld, 1976, emend. Storch 1981)
    - *Cyclopes* Gray, 1821 (= *Cyclothurus* Lesson, 1842, ex Gray, 1825). Rezent; Süd- und Mittelamerika
    - *Palaeomyrmidon* Rovereto, 1914. Pliozän; Argentinien

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Wir danken vielmals Herrn Dr. G. Jores, Darmstadt, für die neuerliche Ausleihe des Typus-Skeletts von *Eurotamandua*, Frau A. Helfricht, Forschungsinstitut Senckenberg, für die zeichnerische Ausführung von Abb. 1–2 und Frau Dipl.-Biol. R. Rabenstein, Forschungsinstitut Senckenberg, für Hilfe beim Röntgen. Der Deutschen Forschungsgemeinschaft danken wir aufrichtig für Sachbeihilfen (Az Sto 104/7–1, 2).

Zusammenfassung

Radiologische Untersuchungen des Typus-Skelettes von *Eurotamandua joresi* aus dem Mittel-Eozän der Grube Messel, Hessen, Deutschland, erbrachten den Nachweis von zwei auffälligen Schädelmerkmalen: 1. Die Pterygoidea sind wie bei heutigen Ameisenbären enorm verlängert und bilden horizontale Gaumenplatten aus; hierdurch sind die Choanen weit in den occipitalen Bereich zurückversetzt (= Autapomorphie der Unterordnung Vermilingua). 2. Wie bei den heutigen Gattungen *Tamandua* und *Myrmecophaga* ist eine akzessorische Bulla tympanica, die vor dem Cavum tympani liegt, ausgebildet (= Autapomorphie der Familie Myrmecophagidae). Beides wird im Kontext der Myrmecophagie gesehen: Der verlängerte knöcherne Gaumen unterstützt den Nahrungstransport zum Schlund und ist Trennwand gegenüber der Nasenhöhle; die hypotympanale Nebenhöhle ist eine akustische Anpassung an die Perkussion harter Insektenbauten und wirkt möglicherweise als Helmholtz-Resonator. Es werden die Osteologie von Gehör- und Pterygo-Alisphenoidregion rezenter Vermilingua beschrieben, Unterschiede zwischen *Eurotamandua* und *Manis* (Pholidota) angeführt und eine Klassefikation der Vermilingua vorgeschlagen. Ameisenbären müssen bereits tief in der Kreidezeit von einer gemeinsamen Xenarthra-Wurzel abgezweigt sein, und auch die basale Dichotomie innerhalb der Vermilingua in Myrmecophagidae und Cyclothuridae ist noch in der Kreidezeit anzusetzen.

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Der erste Fund von *Macaca* (Cercopithecidae, Primates) im Jungpleistozän von Mitteleuropa

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Abstract

The first find of Macaca (Cercopithecidae, Primates) in the Late Pleistocene of Central Europe

Described the left lower first premolar of a male *Macaca* sp., *sylvanus* group, associated with a Würmian thanatocoenosis from the Kugelsteinhöhle II in the Eastern Alps near Graz, Austria. It is the first evidence of a primate in the Late Pleistocene of Central Europe except for *Homo*. As a comparison to the find, the variability of the tooth in the recent Barbary Ape *M. sylvanus* is outlined. The peculiar morphology including the shape of the fossil could not be observed in 14 recent individuals.

Einleitung

Fossile Reste der Gattung *Macaca* Lacépède, 1799 sind aus rund 50 europäischen Fundstellen bekannt und belegen dessen Verbreitung zwischen älterem Pliozän und Jungpleistozän bis fast 53° nördlicher Breite (Norfolk, England) und im Osten bis in den südlichen Kaukasus (Franzen 1973; Szalay und Delson 1979; Ardito und Mottura 1987). Die Funde sind meist singulärer Art; Gebißreste und postcraniale Skeletteile sind selten assoziiert aus einer Fundstelle bekannt (vgl. Fladerer 1987), sodaß seit dem ersten Fund eines fossilen Restes von *Macaca* in Europa (Owen 1845) zahlreiche Namen in der Literatur Einzug gefunden haben – auch die generische Zuordnung betreffend. Nach Sichtungen des jeweils bekannten Gesamtumfangs des Materials in jüngerer Zeit ist nach Szalay und Delson (1979) anzunehmen, daß alle west-, mittel- und osteuropäischen Funde des Plio/Pleistozäns zu einer einzigen, mit der rezenten *M. sylvanus* konspezifischen Art zu stellen sind. In den pleistozänen Thanatozönosen überwiegen generell wärme- bzw. waldliebende Arten. In Analogie zur rezenten Verbreitung der Makaken wurden sie als Leitform der Warmzeiten angesehen (Bartolomei 1969). Eine Arealerweiterung in kaltgemäßigte Habitate kann allerdings angenommen werden (vgl. Singer et al. 1982; Tillier und Vandermeersch 1976). Die bislang jüngsten Hinweise auf eiszeitliche Affen in Europa nördlich des europäischen Mediterrans wurden dem späten Mittelpleistozän zugeordnet (Adam 1975; Carls et al. 1988).

Material und Methode

Fundort

Der fossile Zahn wurde während einer Sondierungsgrabung in der Kugelsteinhöhle II bei Deutschfeistritz („Tropfsteinhöhle am Kugelstein", 15°20′17″ östlicher Länge, 47°13′29″ nördlicher Breite, 478 m ü. M.) aus gestörten Sedimenten geborgen. Der Kugelstein liegt im Nord-Süd-gerichteten Durchbruchstal der Mur im Steirischen Randgebirge, 22 km nördlich von Graz (Abb. 1) (Fuchs 1989; Fladerer 1989).

Der Cercopithecidenzahn wird mit den übrigen Tierresten der Kugelsteinhöhle II am Steiermärkischen Landesmuseum „Joanneum" in Graz, Raubergasse 10 unter der Inventarnummer 73.367 aufbewahrt.

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0 50 100 km
Hunas
Stuttgart
Heppenloch
München
Deutsch-Altenburg
Wien
Deutschfeistritz
Graz

Abb. 1. Fundorte pleistozäner Makaken im Bereich der Ostalpen (Berglandbereich über 500 Höhenmeter schematisiert)



Abb. 2. Macaca sp. der *sylvanus*-Gruppe, linker vorderer unterer Prämolar, Jungpleistozän, Kugelsteinhöhle II bei Deutschfeistritz, Steiermark. a: Lingualansicht, b: Buccalansicht, c: Occlusalansicht. Balken = 3 mm. (Zeichnung: N. FROTZLER, Institut für Paläontologie der Universität Wien)

Vergleichsmaterial

Es standen die Mandibeln von 7 Männchen und 7 Weibchen der rezenten *M. sylvanus* aus folgenden Sammlungen zur Verfügung: Naturhistorisches Museum Wien (NHMW), Institut für Paläontologie der Universität Wien (UWPI), Zoologische Staatssammlung München (ZSSM) und Institut für Palaeoanatomie, Domestikationsforschung und Geschichte der Tiermedizin der Universität München (IPDM).

Das fossile Vergleichsmaterial umfaßt zwei Abgüsse: 1. „*Macaca florentina*", Fundort Strette, Mittelitalien, Altpleistozän, Naturhistorisches Museum Basel V.A.352, 2. „*Macaca* cfr. *sylvanus*" Fundort Grotta Valdemino, Oberitalien, Mittelpleistozän, Università di Ferrara, Dipartimento di Scienze Geologiche e Paleontologiche.

Messungen

In Anlehnung an die bei höheren Primaten verwendeten Meßstrecken (Remane 1927) haben sich für den P_3 von *Macaca* folgende Strecken als brauchbar erwiesen (Abb. 3,3; 4,3). Es wurde an der linken und der rechten Zahnposition gemessen.

1. Obere Länge (L): Größte mesio-distale Länge parallel zur Hauptschneide (vordere und hintere Protoconid-Randleiste), d. h. parallel zur Längsachse, in der Projektion von occlusal gemessen. Diese Meßstrecke scheint identisch mit der „größten Länge des ersten Prämolaren" bei Lampel (1963) und der „Außenlänge" bei Remane (1927).
2. Größte Breite (B): Gemessen in der Horizontalebene normal zur Hauptschneide (Längsachse). Die Strecke liegt entsprechend der Querstellung des Zahns in der Zahnreihe in mesiobuccal-distolingualer Richtung. Die Meßstrecke entspricht der Breite bei Remane (1927).
3. Außenhöhe (H): Gemessen an der Buccalseite zwischen dem tiefsten Punkt der Schmelzgrenze zur Hinterwurzel bis zur Spitze des Haupthöckers. Mit Einschränkung ist die rekonstruierte Protoconidspitze für ein Richtmaß zu verwenden.

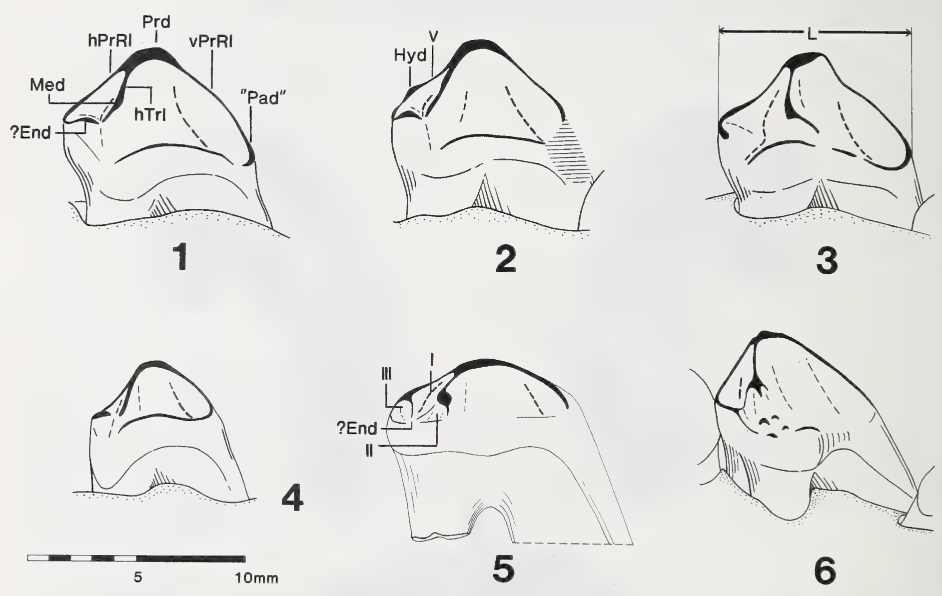


Abb. 3. Schematisierte Lingualansichten des P_3 sin. von *Macaca sylvanus* (rezent), *Macaca* sp. (Jungpleistozän, Österreich) und „*M. florentina*" (Altpleistozän, Italien); 1–3: *M. sylvanus*, männlich, UWPI 1324, NHMW 2614, NHMW 4408; 4: *M. sylvanus*, weiblich, NHMW 2616; 5: *Macaca* sp., männlich, Kugelsteinhöhle II, Steiermark; 6: „*M. florentina*", Strette, Val d'Arno, Altpleistozän, NHM Basel V.A.352, spiegelbildlich. Abkürzungen: Ci = Cingulum, End = Entoconid, iHl = innere Hauptleiste, hMeHl = hintere Metaconid-Hauptleiste, hPrRl = hintere Protoconid-Randleiste, hTrl = hintere Trigonidleiste, (= Protolophid), Hyd = Hypoconid, L = Meßstrecke der oberen Länge, Med = Metaconid, „Pad" = Paraconid-Bezirk, Prd = Protoconid, Tag = Talonidgrube, Trg = Trigonidgrube, V = Vallis externus, Außental (= Hypoflexid), vEnRl = vordere Entoconid-Randleiste, vPrRl = vordere Protoconid-Randleiste; I, II, III = Teilgruben der Talonidgrube

4. Höhe der mesiobuccalen Schmelzvorbuchtung, vordere Höhe (VH): Größte Länge des Schmelzlappens zwischen Protoconidspitze und ventraler Schmelz-Dentin-Grenze.

Der Längen-Breiten-Index (B × 100/L) gibt Vergleichszahlen für den Umriß der Zähne in der Occlusalansicht.

Mit dem Vorderhöhe-Längen-Index (L × 100/VH) läßt sich die relative Höhe der mesiobuccalen Schmelzvorbuchtung darstellen.

Ergebnisse

Morphologie des Fossilfundes

Der vorliegende Zahn ist der vordere Prämolar einer linken Mandibel (P_3 sin.). Die hohe Schmelzvorbuchtung und der längsgestreckte Umriß weisen ihn einem männlichen Tier zu. Der Zahn ist bis auf die Spitze der hinteren Wurzel vollständig erhalten (Abb. 2). Die Abkauung ist stärker fortgeschritten, die Zahnkrone erscheint über ihre gesamte Fläche attritiert. Die hellgraue bis graublaue Färbung des intakten Zahnschmelzes kontrastiert auffallend mit der mittel- bis schwarzbraunen Färbung der Wurzeln und des Dentinkerns in der Kaumarke der Krone. Aus dem Umriß des großen Dentinfeldes im zentralen Bereich (Abb. 2c) und der schmalen Fahnen nach mesial und distal kann auf die Morphologie des nicht attritierten Stadiums geschlossen werden (Abb. 3,5; 4,7).

Für die morphologischen Bezeichnungen wird hier die von Remane (1960) vorgeschlagene Terminologie verwendet. Schwierigkeiten in der Homologisierung veranlaßten zum

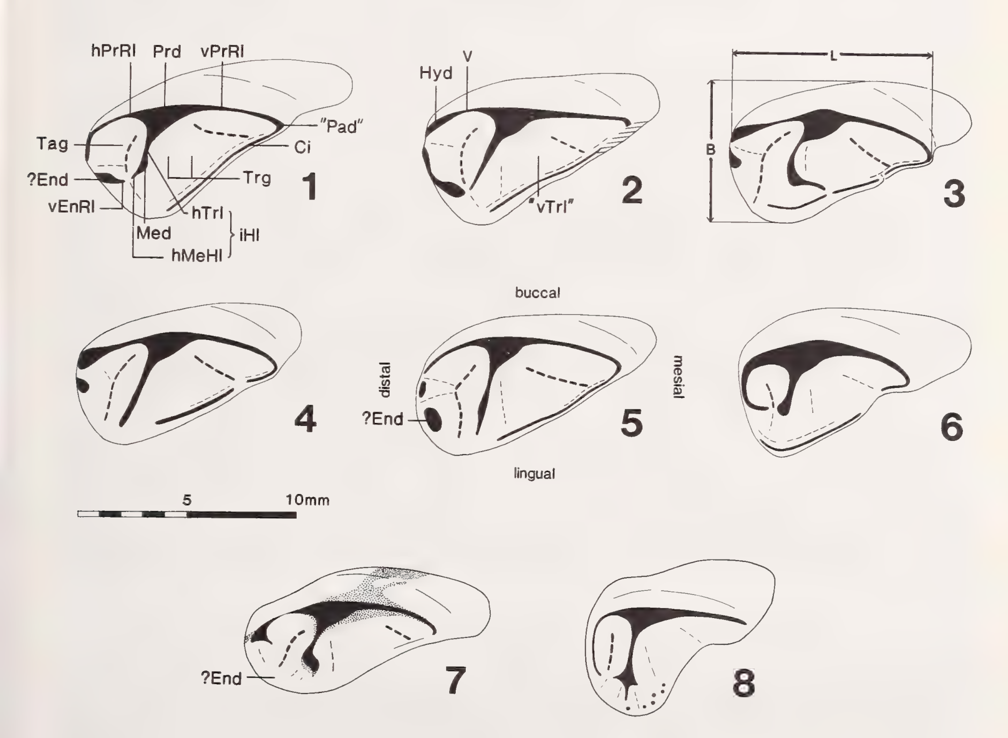


Abb. 4. Schematisierte Occlusalansichten des P_3 sin. von männlichen *M. sylvanus* (rezent), *Macaca* sp. (Jungpleistozän, Österreich) und „*M. florentina*" (Altpleistozän, Italien). 1–6: *M. sylvanus,* rezent. 1: UWPI 1324; 2: NHMW 2614; 3: NHMW 4408; 4: IPDW Nr. 4; 5: NHMW 2614 spiegelbildlich; 6: NHMW 32990; 7: *Macaca* sp., Kugelsteinhöhle II, Steiermark, Jungpleistozän; 8: „*M. florentina*", Strette, Val d'Arno, Altpleistozän, NHM Basel A.V.352, spiegelbildlich. (Abkürzungen siehe Abb. 3)

Verweis auf die Terminologie von KAY (1977; siehe auch SZALAY und DELSON 1979: Fig. 159).

Die größte Ausdehnung des zentralen Dentinfeldes zeigt die Lage eines primär deutlichen Protoconids an (Abb. 4,7). Einer der Ausläufer des Protoconidfeldes, die als dunkelbraune Verfärbung unter dem ausgedünnten Schmelz sichtbar sind, erstreckt sich nach mesial. Seine Position entspricht der vorderen Trigonid-Randleiste, die in einem früheren Stadium deutlich ausgeprägt gewesen sein mußte. Ein rund 0,2 mm breiter, brauner Dentinstreifen zieht, vom Haupthöcker ausgehend, nach distolingual und bildet eine notenkopfartige Verdickung nach lingual. Dieses Feld liegt in der Position des Metaconids (Abb. 3,5). An den Unterkiefermolaren der Catarrhinen vermittelt zwischen Protoconid und Metaconid die hintere Trigonidleiste (Protolophid bei KAY 1977), nach distal die hintere Protoconid-Randleiste (Abb. 4,1; 4,7). In der Buccalansicht ist eine Einsattelung der mesio-distalen Hauptschneide erkennbar (Vallis externus, Außental oder Hypoflexid; Abb. 3,5). Die Lingualfläche des Trigonids (Trigonidgrube) wird von einem breiten niederen Rücken in eine vordere breite und eine hintere schmale Furche gegliedert. Beide zeigen in sich kleine kraterartige Vertiefungen und eine seichte Runzelung.

Der distale Bereich der Krone ist sehr kurz und deutlich strukturiert. In der Lingualecke ist eine Erhebung festzustellen, die vom Basalband nicht abgesetzt ist. Von dieser zweigen zwei feine Grate in Richtung Hypoconid und Metaconid ab. Der nach mesial gerichtete Grat ist unmittelbar vor dem Metaconid abgesetzt (Abb. 2c). Eine vergleichbare Position nimmt am Molaren der Catarrhinen nach REMANE (1960) die vordere Entoconid-Randleiste ein. Der zweite Grat dieses als Entoconid vermuteten akzessorischen Höckers ist mit dem Hypoconid verbunden (hintere Talonid-Randleiste).

Durch das niedrige Leistensystem entstehen am Talonid drei Gruben (Abb. 3,5: I–III). Den größten Anteil hat eine furchenartige Vertiefung (I). Lingualwärts liegt eine kleinere, etwa dreieckige Grube (II), die in sich durch einen kurzen vom Metaconid ausgehenden leistenförmigen Fortsatz in der vorderen Hälfte gegliedert wird. Eine annähernd gleich große runde Grube (III) liegt zwischen Hypoconid und „Entoconid".

Ein breites Basalband umgibt die Krone von der mesialen Ecke der Lingualseite bis unter das Hypoconid. Es läßt sich nicht feststellen, ob hier in einem Stadium ohne Abkauung eine durchgehende Furche das Basalband nach oben abgegrenzt hat. Die mäßig konvexe Hauptfläche des mesiobuccalen Schmelzlappens ist durch Attrition abgeflacht. Dunkelbraunes Dentin schimmert durch den intakten blaugrauen Schmelz. Sowohl an der Lingualseite als auch am buccodistalen Rand zur Vorderwurzel liegt der Schmelzlappen wulstartig über der Vorderwurzel. Am unteren Ende ist die Schmelz-Dentin-Grenze durch eine kleine Einbuchtung unregelmäßig gelappt.

Der Zahn hat zwei Wurzeln. Die vollständig erhaltene Vorderwurzel hat einen länglich ovalen Querschnitt. An der Lingualseite ist eine rund 1,5 mm lange kerbenartige Vertiefung 3 mm oberhalb der Wurzelkanalöffnung zu beobachten. Die Spitze der hinteren Wurzel ist abgebrochen. Die Bruchkante ist fein zugerundet. Der verdrückt ovale Querschnitt in der Bruchebene hat einen Längsdurchmesser von 2,8 mm und eine Breite von 2,1 mm.

Vergleich

Der Vergleich von 14 Individuen der rezenten *M. sylvanus* und den P_3 von drei fossilen Vertretern aus dem Pleistozän zeigt folgende Variabilität der Kronenmorphologie:

Das Protoconid liegt meist im mittleren Drittel des mesiodistalen Hauptgrates. Im Fall der altpleistozänen „*M. florentina*" aus Strette liegt der Haupthöcker in der hinteren Kronenhälfte (Abb. 3,6).

Die hintere Trigonidleiste (Protolophid) zeigt Variationen in ihrer Länge; das Metaconid zeigt Variationen in seiner Position und seiner Höhe. Der Grat kann bis zur Linguodistalecke reichen (Abb. 4,4; 5,1), sehr kurz (Abb. 4,1; 4,6) oder auch nach mesial geknickt

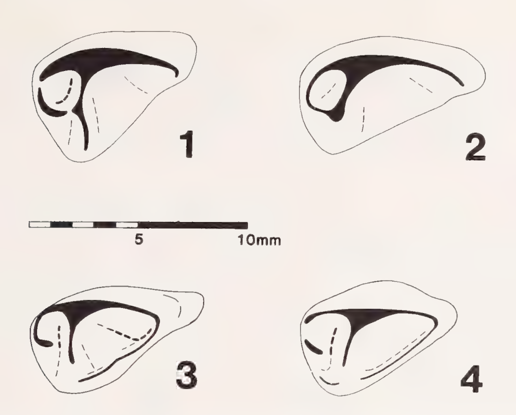


Abb. 5. Schematisierte Occlusalansichten des P_3 sin. von weiblichen *M. sylvanus,* rezent. 1: NHMW 2615; 2: NHMW 3422; 3: NHMW 2616; 4: ZSSM 1959/4

sein (Abb. 4,3; 4,7). Das Metaconid kann sehr nahe am Haupthöcker liegen (Abb. 4,2) oder von diesem deutlich abgesetzt sein (Abb. 4,8). Bei der altpleistozänen „*M. florentina*" bildet das Protolophid einen konkaven Grat. Das Metaconid über der lingualen Wurzel ist gut entwickelt (es ist am Abguß nicht feststellbar, ob hier Dreiwurzeligkeit vorliegt oder die hintere Wurzel linguo-buccal stark verbreitert ist). Runzelungen gehen vom Nebenhöcker zum Lingualrand aus. Dieser ist durch kleine Höckerchen skulpturiert. Häufig ist ein Grat ohne Höckerdifferenzierung zu beobachten (Abb. 4,4; 5,4). Als eine Verbreiterung der hinteren Trigonidleiste ist das Metaconid eines Magotweibchens (Abb. 5,3) angedeutet.

Die Lingualfläche des Trigonids wird von einer breiten Furche im vorderen Bereich zweigeteilt. Eine hintere, zweite, kann angedeutet sein. Häufig ist eine Runzelung der Lingualfläche zu beobachten. Seltener ist die Lingualfläche ungegliedert (Abb. 5,4). Ein Basalband kann die Fläche zur Wurzel hin begrenzen. Es fehlt bei den weiblichen Zähnen in Abb. 5,1 und Abb. 5,2.

Den Distalbereich nimmt im einfachsten Fall eine Talonidgrube ein, die nach lingual offen ist. Eine fast oder ganz geschlossene kleine Trigonidgrube scheint häufig aufzutreten (Abb. 3,1; 4,1). Eine einfache rundliche Talonidgrube mit Furche nach lingual (Abb. 5,1), kann auch am Mandibelfragment eines weiblichen Tieres aus dem Mittelpleistozän der Grotta Valdemino festgestellt werden. An einem männlichen Magot vom „Affenberg" in Sélestat, Oberrhein (IPDM Nr. 2) ist die Talonidgrube des linken P_3 viel deutlicher allseitig von Graten abgegrenzt als am rechten. Die asymmetrische Anlage ist auch aus den divergierenden Maßen der linken und rechten Seite (Tab. 1) zu erkennen. Ein weiterer bemerkenswerter Typ ist die kurze querfurchenartige Talonidgrube beim altpleistozänen Makaken (Abb. 4,8).

Das Hypoconid tritt durch eine Einsattelung (Außental) im distalen Bereich der Hauptkante häufig deutlich hervor (Abb. 3,2; 4,2). Vom Hypoconid abgesetzt ist häufig ein kleiner akzessorischer Höcker, der dem Entoconid homolog sein dürfte (Abb. 3,1; 4,1). Fast ebenso oft fehlt ein Höcker im distalen Grat (Abb. 3,6; 4,8). Eine Aufgliederung in zwei Höcker lingual des Hypoconidareals war nur einmal zu beobachten (Abb. 4,5).

Auskunft über die Größenverhältnisse des P_3 geben die Tabelle und Abb. 6. Die Mittelwerte der Geschlechtergruppen sind in Zeile 11 für die Männchen und in Zeile 19 für die Weibchen gegeben. Am Vorderlappen-Längen-Verhältnis lassen sich die Geschlechter gut unterscheiden; die geringere Länge der Schmelzvorbuchtung bei den Weibchen kommt im größeren Vorderhöhe-Längen-Verhältnis zum Ausdruck.

Maße des ersten unteren Prämolaren von *Macaca* der *sylvanus*-Gruppe

Angaben in mm. Zeilen 4 bis 10 (männliche) und 12 bis 18 (weibliche) rezente *M. sylvanus* aus vier Sammlungen (siehe Text). Abkürzungen: L = obere Länge, B = größte Breite, H = Außenhöhe, VH = Höhe der Schmelzvorbuchtung, M = Mittelwert, s = Standardabweichung. In Klammern rekonstruierte Maße, die den Abkauungsgrad berücksichtigen

			L	B	H	VH	$\frac{B \times 100}{L}$	$\frac{L \times 100}{VH}$
1.	*Macaca* sp. Kugelstein, Jungpleistozän ♂ adult/senil		8.5	5.5	5.4 (6.9)	14.2 (15.3)	64.7	(55.6)
2.	„*Macaca* cfr. *sylvanus*" Grotta Valdemino, Mittelpleistozän ♀ adult		5.7	4.8	5.3	?	84.2	?
3.	„*M. florentina*" Strette, Altpleistozän ♂ adult		7.9	6.4	6.7	14.7	81.0	53.7
4.	*M. sylvanus* rez.	sin.	8.7	6.9	7.1	15.5	79.3	56.1
	UWPI 1324, ♂ adult	dext.	8.9	6.8	7.3	15.5	76.4	57.4
5.	*M. sylvanus* rez.	sin.	7.9	6.5	6.9	14.3	82.3	55.2
	NHMW 2614, ♂ adult	dext.	8.5	6.3	7.8	15.5	74.1	54.8
6.	*M. sylvanus* rez.	sin.	8.5	7.4	7.4	13.6	87.1	62.5
	NHMW 4408, ♂ subadult	dext.	8.6	7.4	6.9	13.8	86.0	62.3
7.	*M. sylvanus* rez.	sin.	7.2	5.2	6.1	12.9	72.2	55.8
	NHMW 32990, ♂ adult	dext.	7.6	5.2	5.9	13.5	68.4	56.3
8.	*M. sylvanus* rez.	sin.	7.0	5.9	7.2	12.0	84.3	58.3
	IPDM Nr. 2, ♂ adult	dext.	6.6	5.5	6.6	12.7	83.3	52.0
9.	*M. sylvanus* rez.	sin.	7.6	5.5	7.5	14.7	72.4	51.7
	IPDM Nr. 4, ♂ adult	dext.	8.0	5.5	7.2	14.3	68.8	55.9
10.	*M. sylvanus* rez.	sin.	7.2	5.9	(6.7)	(15.2)	81.9	(47.4)
	ZSSM o. Nr., ♂ senil	dext.	8.4	6.2	(6.5)	(14.3)	73.8	(58.7)
11.	*M. sylvanus*	M	7.9	6.2	6.9	14.1	77.9	56.0
	7 ♂♂, Mittelwert	s	0.7	0.8	0.5	1.1	6.4	4.0
12.	*M. sylvanus* rez.	sin.	6.2	5.2	5.3	9.1	83.9	68.1
	NHMW 2615, ♀ adult	dext.	6.3	4.9	5.3	9.5	77.8	66.3
13.	*M. sylvanus* rez.	sin.	5.9	4.4	5.3	8.8	74.6	67.0
	NHMW 2616, ♀ adult	dext.	5.5	4.5	5.5	9.0	81.8	61.1
14.	*M. sylvanus* rez.	sin.	6.3	4.7	5.2	9.9	74.6	63.6
	NHMW 34222, ♀ adult	dext.	6.2	5.3	5.4	9.8	85.5	63.3
15.	*M. sylvanus* rez.	sin.	5.6	5.0	(4.8)	(8.1)	89.3	(69.1)
	IPDM Nr. 1, ♀ adult	dext.	5.6	4.9	(4.9)	(8.2)	87.5	(68.3)
16.	*M. sylvanus* rez.	sin.	5.8	4.7	(4.6)	(9.4)	81.0	(61.7)
	IPDM Nr. 3, ♀ senil	dext.	5.8	4.7	(4.4)	(9.4)	79.3	(61.7)
17.	*M. sylvanus* rez.	sin.	5.8	4.8	5.5	10.9	82.8	53.2
	ZSM 1959/4, ♀ subadult	dext.	6.1	5.1	5.5	9.7	83.6	62.9
18.	*M. sylvanus* rez.	sin.	5.7	4.1	–	–	71.9	–
	ZSM AM/1423, ♀ senil	dext.	–	–	–	–	–	–
19.	*M. sylvanus*	M	5.9	4.8	5.1	9.3	81.0	63.9
	7 ♀♀ Mittelwert	s	0.3	0.3	0.4	0.8	5.2	4.4

Der erste untere Prämolar von *M. sylvanus* zeigt eine ähnlich große Variabilität in Abmessungen und Morphologie, wie sie bei *Cercopithecus* (Lampel 1963) und bei Pongiden (Remane 1960) beobachtet wird.

Es können Unterschiede in den Abmessungen bis über 15 % zwischen linker und

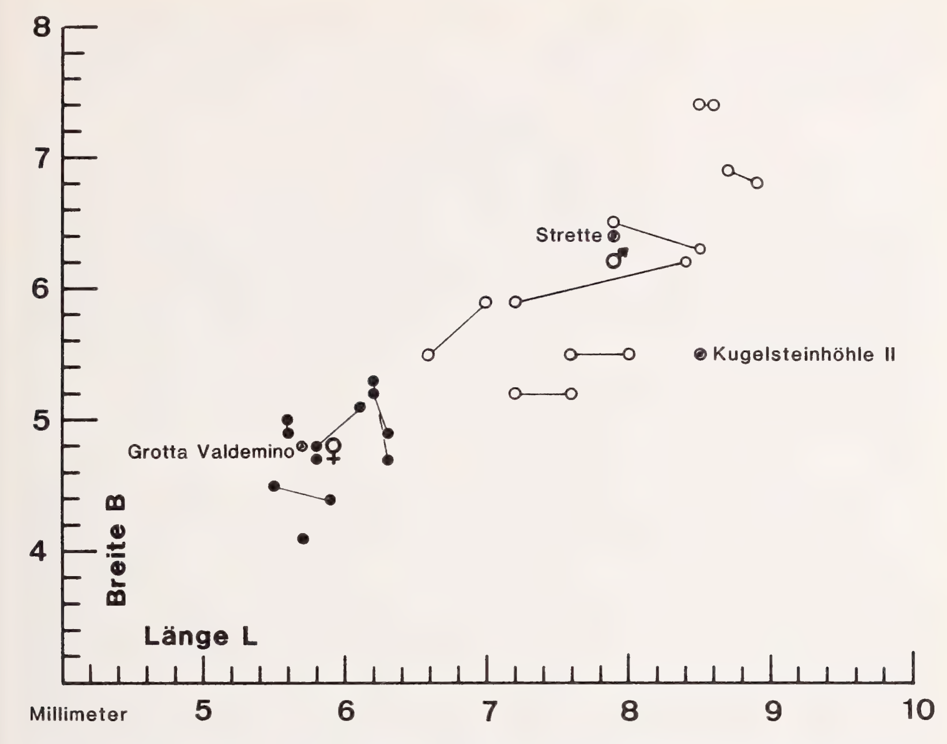


Abb. 6. Breiten-Längen-Verhältnis der P_3 von *Macaca* der *sylvanus*-Gruppe (vergleiche Tabelle), Werte der linken und rechten Zahnposition der rezenten Individuen verbunden. ○ = männliche Tiere, ● = weibliche Tiere. Die Geschlechter-Symbole kennzeichnen die Mittelwerte der rezenten Individuen

rechter Seite am Individuum und Unterschiede zwischen linker und rechter Seite im Kronenrelief beobachtet werden.

Der Cercopithecidenzahn aus der Kugelsteinhöhle liegt in der mesio-distalen Länge im oberen Bereich der Variationsbreite der rezenten *M. sylvanus* (Abb. 6). Das Vorderhöhe-Längen-Verhältnis von 55,6 entspricht den männlichen Magots. Die vergleichsweise geringe Breite des fossilen Zahnes führt zu einem Breiten-Längen-Verhältnis, das ihn von den rezenten Individuen und noch deutlicher von „*M. florentina*" aus Strette (64,7 gegenüber M = 77,9 bzw. 81,0) unterscheidet. Auffallend ist die große Breite des altpleistozänen Zahnes. Szalay und Delson (1979: Abb. 177A, 177F) bilden Mandibeln von *M. s. florentina* aus dem Oberpliozän bzw. *M. s. prisca* aus dem Unterpliozän ab, an deren P_3 ebenfalls konkave Lingualseiten, große Breite und eine echte Distalseite wie am Strette-Exemplar zu finden sind. Es wäre zu überprüfen, ob sich in diesem Merkmal die plio/pleistozänen Funde von der rezenten Art unterscheiden lassen.

Der fossile Zahn eines Makakenmännchens aus der Kugelsteinhöhle zeigt Eigentümlichkeiten, deren Kombination ihn von den rezenten Individuen von *M. sylvanus* unterscheiden: geringere Breite und geringeres Längen-Breiten-Verhältnis, sehr deutlicher distaler Höcker (Hypoconid), dreigeteilte Talonidgrube, akzessorischer Höcker in der distolingualen Ecke in deutlicher Entfernung vom Hypoconid (vermutliches Entoconid). Morphologie und Breitenmaß liegen etwas außerhalb der beobachteten Variationsbreite von 14 (männlichen und weiblichen) bzw. 7 (männlichen) Individuen der rezenten *M.*

sylvanus. Aufgrund der Unterschiede wird hier eine Zuordnung als *Macaca* sp. des *sylvanus*-Formenkreises vorgenommen.

Diskussion

Zeitliche Zuordnung

Da der Zahn aus einer gestörten Sedimenteinheit der Kugelsteinhöhle stammt, kann nur indirekt auf sein Alter geschlossen werden. Die blaugraue Färbung des Zahnschmelzes stimmt mit jener der Fossilreste des tiefsten angetroffenen Horizontes überein. Von diesem kann folgende vorläufige Artenliste angegeben werden: *Phyrrocorax* sp., *Talpa europaea,* Chiroptera indet., *Marmota marmota, Clethrionomys glareolus, Arvicola terrestris, Microtus malei, M. nivalis, M. arvalis, M. agrestis, M. gregalis, Hystrix* sp., *Lepus* sp., kleiner Mustelide, größerer Mustelide, *Ursus spelaeus, U. arctos, Canis lupus, Vulpes vulpes, Panthera pardus, Sus scrofa, Megaloceros giganteus, Cervus elaphus,* kleiner Cervide, *Capra ibex, Bos primigenius, Bison priscus.* In der Assoziation ist das Auftreten von Waldformen neben indifferenten Arten und Tieren der offenen Landschaft zu beobachten. Der sedimentologische Befund weist auf eine fluviatile Genese, so daß angenommen werden kann, daß in der Assoziation verschieden alte Thanatozönosen vertreten sind. Nach Jánossy (1986) erlaubt *Hystrix vinogradovi* als „index fossil" eine Zuordnung ins Riß-Würm-Interglazial. Der Nachweis von *Quercus* und *Carpinus* in Holzkohlefragmenten (Schneider in Fuchs 1989) stützt zumindest die Interpretation eines klimatisch gemäßigten Lebensraumes. Aus dem Steirischen Randgebirge sind Sedimente, die biostratigraphisch vor-rißzeitlich bis rißzeitlich datiert werden, nur aus der rund 4 km entfernten Repolusthöhle bekannt (Mottl 1975). Da aus Höhlen des Kugelsteins kein einziger Hinweis auf ein höheres Alter als frühes Würm vorliegt, wird hier ein hypothetisches Alter der Population einer mit dem rezenten Berberaffen nahe verwandten oder konspezifischen Art zwischen dem Eem-Interglazial und dem älteren Würm-Glazial angegeben, einem Zeitraum zwischen rund 128 000 und rund 75 000 Jahren vor heute (vgl. Labeyrie 1984; Abb. 5).

Verbreitungsgeschichtliche Bedeutung

Der phylogenetische Zusammenhang der fossilen Funde in Europa mit dem heute in Nordafrika in Reliktarealen beheimateten Magot ist noch nicht geklärt. Die Nominatform *M. sylvanus* dürfte in Nordwestafrika seit dem Plio/Pleistozän kontinuierlich verbreitet gewesen sein (Starck 1990). Die ältesten Funde von Makaken in Europa werden von Delson (1980) in Verbindung mit dem Messinischen Ereignis am Ende des Miozäns gebracht: die teilweise Austrocknung des Mittelmeeres ermöglichte eine Ausbreitung der Gattung nach Europa und eine einheitliche circummeditarrane Besiedelung von *M. sylvanus.* Osteologische und odontologische Unterschiede zwischen den fossilen Formen können beobachtet werden (Thenius 1965; Franzen 1973; Szalay und Delson 1979; Fladerer 1987). Sie sollen nach Delson (1980; Delson und Brooks in Tattersall et al. 1988) innerhalb der artlichen Variabilität der Nominatformen liegen. Die Systematik der rezenten Arten beruht fast ausschließlich auf deren Weichteilanatomie (Hill 1974; Fooden 1976). Osteologische Vergleiche stehen noch aus. In diesem Zusammenhang sind auch Delsons Untersuchungen zu sehen, denen zufolge er die europäischen Formen zwischen dem Ruscinium (5–4 Ma) und dem Mittelpleistozän chronosubspezifisch aufteilt (Szalay und Delson 1979; Delson 1980): *M. s. prisca, M. s. pliocena, M. s. florentina* und als mögliche Kleinform im Oberpliozän Sardiniens *M.? sylvanus majori,* der jedoch am ehesten der Rang einer echten Morphospezies als *M. majori* zukommen dürfte (vgl. Starck 1990). Eine kontinuierliche Besiedelung des südiberischen Raumes ist paläontologisch nicht belegt (vgl. Hill 1974). Somit ist auch nicht erwiesen, ob das ursprüngliche

europäische Vorkommen auf Gibraltar eine Restpopulation des hypothetischen circummediterranen Verbreitungsareals darstellte.

Mittelpleistozäne Makakenpopulationen sind aus England, aus Deutschland (Bilzlingsleben – MANIA 1990 –, Mosbach 2, Heppenloch, Hunas), aus dem südfranzösisch-iberischen Raum und aus Italien (ARDITO und MOTTURA 1987) nachgewiesen. Die der Kugelsteinhöhle nächstgelegene Fundlokalität ist Bristie im Karst von Triest (BARTOLOMEI 1980) in 210 km Entfernung. Evolutionsstratigraphischen Vergleichen an Arvicoliden-Faunen zufolge werden für die bisher jüngsten mitteleuropäischen Affenfunde Angaben zwischen 320 000 und 210 000 Jahren vor heute gemacht (CARLS et al. 1988). Jungpleistozäne Populationen von Makaken sind bisher von der Solana del Zamborino bei Granada (MARTÍN PENELA 1986), von Cova negra bei Valencia (PÉREZ RIPOLL 1977), von Torre di Pietra bei Rom (ARDITO und MOTTURA 1987) und aus dem südlichen Kaukasus (VERESHCHAGIN 1959; LIOUBIN und BARYCHNIKOV 1984) bekannt. Die mit Höhlenbärenresten assoziierte Makakenmandibel aus der Grotta Valdemino bei Borgio, Oberitalien (TOZZI 1969), ist nach SALA (pers. Mitteilung von 7/1990) aufgrund der Begleitfauna (*Homotherium* sp., *Ursus* cf. *deningeri, Allocricetus bursae, Pliomys episcopalis* u. a.) als mittelpleistozän einzustufen. Das Fundgebiet des steirischen Makaken, der hier zur *sylvanus*-Artengruppe gestellt wird, war niemals vergletschert. Die geringste Entfernung zu einer würmzeitlichen Lokalvergletscherung betrug etwa 22 km, zum alpinen Eisstromnetz etwa 50 km (vgl. Beilage in HUSEN 1987). Geomorphologischen Beobachtungen zufolge war die Vergletscherung der Ostalpen im Riß-Hochglazial noch um einige Kilometer weiter ausgedehnt, so daß an eine eemzeitliche Wiederbesiedelung gedacht werden müßte. Die sedimentologischen Befunde der südostfranzösischen altpleistozänen Makaken-Fundstelle Vallonet (TILLIER und VANDERMEERSCH 1976; PÉREZ RIPOLL 1977) und das gemeinsame Vorkommen von *Macaca* und *Lemmus lemmus* in mittelpleistozänen Sedimenten Ostenglands (SINGER et al. 1982) sprechen jedoch für Habitate auch unter borealem Klima. Somit erscheint auch die Permanenz mittelpleistozäner Populationen im südlichen Mitteleuropa möglich.

Der Fundzusammenhang des hier beschriebenen Cercopithecidenzahnes mit Artefakten in Moustérien-Fazies (MOTTL 1975; FUCHS 1989) macht ein Zusammentreffen paläolithischer Kulturträger und Makaken wahrscheinlich. Ähnliche Befunde stammen aus Ostengland (SINGER et al. 1982), von der mittelpleistozänen *Homo erectus*-Fundstelle Bilzlingsleben (MANIA 1990), dem Acheuléen des südlichen Kaukasus (VERESHCHAGIN 1959; LIOUBIN und BARYCHNIKOV 1984), aus dem älteren Jungpleistozän von Torre in Pietra bei Rom (zit. nach ARDITO und MOTTURA 1987) sowie aus dem Acheuléen und Moustérien des südlichen Spaniens (MARTÍN PENELA 1983; PÉREZ RIPOLL 1977).

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Zusammenfassung

Der Fund eines linken unteren vorderen Prämolaren eines Makakenmännchens aus Sedimenten der Kugelsteinhöhle II bei Deutschfeistritz, Steiermark, ist der erste Beleg für eine Besiedelung des Alpen-Ostrandes durch Cercopitheciden im jüngeren Pleistozän. Archäologischer Befund und paläontologi-

sche Auswertung der begleitenden Thanatozönosen lassen auf ein letztinterglaziales bis würmzeitliches Alter schließen. Der Zahn zeigt im morphologischen und im metrischen Vergleich Unterschiede zum rezenten Magot *Macaca sylvanus* L., an dessen P_3 eine bemerkenswerte Variabilität festgestellt werden kann. Der Fossilfund wird als *Macaca* sp. der *sylvanus*-Gruppe bestimmt.

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Southern Right whale dolphins, *Lissodelphis peronii* off the Pacific coast of South America

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Abstract

Reviewed the distribution and movements of southern right whale dolphins (*Lissodelphis peronii*) off western South America. Data consist of 36 confirmed records from 1823 through 1990, almost half unpublished and including records of specimens taken incidentally in net fisheries, strandings and sightings which could be authenticated. Preliminary surveys suggest that *L. peronii* may be one of the most common cetaceans off northern Chile, where recently gill net entanglements have become alarmingly common. Mean group size was 368. Assessment of population density and fishery mortality is urgently needed. The normal habitat of right whale dolphins off South America appears strictly pelagic. Two specimens caught near Pucusana (12° 30′ S), the second and third confirmed records for Peru, extend the known range north five degrees. North of 25 °S, more records were registered in July–September than in all other months combined, suggesting a northbound migration in austral winter and spring. Off Chile, between 25° and 40° S, right whale dolphins were seen year-round. Distribution extends to at least 170 km offshore north of 40° S and 250 km off the southern Chilean coast; south of Cape Horn it is circumpolar in the West Wind Drift.

Introduction

The southern right whale dolphin, *Lissodelphis peronii* (Lacépède, 1804) is a circumpolar, marginal Antarctic species that is largely found in temperate waters. Although there are a few records south of the Antarctic Convergence, most are more northerly, in and north of the West Wind Drift (Leatherwood and Reeves 1983; Brownell 1974). Over most of the species' known range, well-documented records are generally scarce; possible exceptions are: the SW Pacific, and in particular the New Zealand/Tasmania region, where sightings and strandings have been reported from about 53° S to 35° 30′ S and have been associated with surface water temperatures from 9–17 °C (Fraser 1955; Gaskin 1968a, b; Brownell 1974; Baker 1981); the eastern South Atlantic, where twelve sightings have been reported from a localised area off the west coast of Namibia (Cruickshank and Brown 1981; Findlay 1989). Findlay (1989) suggested these might represent a resident population, associated with the Luderitz upwelling cell in the region. Finally, osteological remains of several tens of southern right whale dolphins were collected by Goodall (1978, 1989) on the coasts of Tierra del Fuego, in the western South Atlantic.

The distribution of right whale dolphins in the Southeast Pacific has been discussed in more or less detail by Fraser (1955), Brown (1973), Brownell (1974), Aguayo (1975) and Donoso-Barros (1975). The species' range was commonly summarized as "from Cape Horn to Arica [northern Chile]" but there actually were less than ten confirmed records for the entire eastern South Pacific. More recent general reviews on the distribution of small cetaceans off Chile and Peru could not add any new data (Sielfeld 1983; Cardenas et al. 1986; van Waerebeek et al. 1988; Majluf and Reyes 1989; Jefferson and Leatherwood 1990; Jefferson et al. 1991).

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In the last few years the number of authenticated specimen and sighting records of southern right whale dolphins in the study area has increased rapidly. It coincided, not surprisingly, with the creation of several centers for cetacean research, e.g. the Santiago-based Red de Avistamiento de Cetáceos (RAC), the Centro de Investigación y Manejo de Mamíferos Marinos (CIMMA) at Valvidia, Chile, and the Centro Peruano de Estudios Cetológicos (CEPEC) at Pucusana, central Peru. In addition, the existing Grupo de Aves y Mamíferos Marinos of the University of Antofagasta, in northern Chile, expanded its research effort on marine mammals.

Published accounts of right whale dolphins from the west coast of South America are barely accessible in such sources as small local journals, conference proceedings and historical papers. The purpose of this paper is to compile and critically review published information while adding new records. Confirmed records are then examined for insight on seasonal movements, distribution centres, boundaries and habitats of right whale dolphins off western South America.

Material and methods

There are 36 confirmed records (20 published and 16 new) of southern right whale dolphins off the Pacific coast of South America, from the year 1823 until 1990, presented below. These include published records only if they offer some clear characterisation of the animal(s) as basis for identification. New accounts were accepted if authenticated by a specimen, a recognisable photograph or a drawing and clear description. For each new record, location of available voucher material is indicated.

Specimens reported from the last few years were found because of extensive beach combings and increased monitoring of fishing port terminals by many different people along coasts of Chile and Peru (e.g. Guerra et al. 1987; Brito and Reyes 1990; Oporto 1990; Torres et al. 1990; van Waerebeek and Reyes 1990). A few specimens collected on Chilean territory in eastern Magallanes, but thought to have originated from the South Atlantic, are not included. Record numbers correspond to those found in Fig. 1. Unless indicated otherwise, record localities are from Chile.

Results

1. Lesson and Garnot (1826) reported having seen right whale dolphins "several times" near Cabo Pillar (52° 43′ S, 74° 42′ W), at the western end of the Strait of Magellan, on their 1822–1825 voyage around the world. The authors failed to mention the exact dates, but from the context it can be deduced that the sightings probably were made in late summer.

2. A clear description of this species, referred to as *"Delphinus Peronii"*, was presented by Bennett (1840) based on several specimens harpooned off South America, one of which measured six feet four inches (193 cm). The author commented on its distribution: "[Right Whale Porpoises] . . . were afterwards frequently seen during our passage round the Horn, and as high as 54°S; but we did not observe them in a lower latitude than 40°S, on the western side of Cape Horn, nur during any subsequent part of the voyage".

3. In their book "Voyage dans l'Amérique méridionale" (1847) d'Orbigny and Gervais (1847) gave the following account of the species under the name *Delphinapterus Peronii:* "We encountered them from 48° to 64°S, around Cape Horn. A harpooned individual permitted us to make a drawing with all its proportions carefully taken . . ." The meticulously figured specimen leaves no doubt about its identity. However, it is uncertain whether it was taken in the Atlantic or the Pacific Ocean. This record, therefore, should be regarded as incertae sedis.

4. Malm (1871), who referred to this species as *Delphinapterus Peronii,* reported on a 185 cm specimen of unspecified sex captured during the Eugenie Expedition at 49° 09′ S, 78° 50′ W on 15 February 1852. The nearly complete skeleton is reportedly at the National

Swedish Museum at Stockholm (originally) labeled "*Delphinus leucorhamphus* Less. Peron".

5. and 6. About 1000 southern right whale dolphins were sighted between 33° and 49°S during three cetacean surveys 25 March–23 December 1966 (Aguayo 1975). The two largest groups observed were about 500–600 at 33° 41′S, 73° 13′W on 3 April, and about 200 at 45° 14′S, 77° 37′W on 21 December. No additional data are presented for these or other sightings.

7. On 12 February 1968, fishermen of Caleta Higuerillas, Concón (32° 55′S), caught a female alive with a hook, half a mile off the coast. After it was examined and photographed the animal was released (Aguayo 1975).

8. From 15 May–6 July 1970, the R/V Hero cruised the southwest and central coasts of Chile and offshore to the Juan Fernández–San Ambrosio Islands for observations of marine mammals and birds. Gilmore (1971) reported *L. peronii* from "only near Golfo de Arauco" in June 1970. Although no description or voucher data are available, the authority of the source is considered convincing.

9. On 17 September 1970, at position 18° 53′S, 71° 43′W, a group of about 50 right whale dolphins travelling southwest was sighted from the SS Pizarro. Sea surface temperature was 17.9 °C (McLean 1971).

10. On 31 January 1970, a herd of about 20 dolphins was seen from the SS Pizarro at 29° 35′S, 71° 45′W. The animals were moving southward. The sea surface temperature was 18.3 °C (Thomas 1970).

11. Torres and Aguayo (1979) gave an account of a 200 cm male harpooned by swordfish fishermen some 10–12 miles off Papudo (32° 30′S) on 5 May 1975. Based on the animal's stomach contents, the authors suggested that the feeding strategy of the southern right whale dolphin may be epipelagic and nocturnal.

12. In February 1980, the carcass of a physically mature specimen of unknown sex was collected from the beach of Cachinales (25° 10′S). The complete skeleton (AMM-024) is at the Instituto de Investigaciones Oceanológicas, University of Antofagasta, in northern Chile (Guerra et al. 1987).

13. One of us (JLB) recovered a neonate (of unknown sex, possibly prematurely born) from the stomach of a 170 cm large Patagonian toothfish or "bacalao de profundidad", *Dissotichus eleginoides,* at the fish market of San Antonio (33° 35′S), central Chile, on 14 October 1983. The predatory toothfish had been caught in a deepsea hook-fishery two or three days earlier, some distance southwest of San Antonio. Although its skin had sloughed from gastric juices, the 86 cm, 5.1 kg, dolphin was otherwise complete. Drawings were made, but unfortunately, except for a few bones (JLBM-CE-8; San Antonio Museum), the specimen itself was lost.

14. A skeleton and skin of this species is kept at the Museo del Departamento de Zoología (MZUC) of the University of Concepción (Ruiz and Oyarzo 1987). The dolphin, a 194 cm male, became accidentally entangled in nets set by local fishermen in Bahía de Concepción (36° 42′S, 73° 02′W) in 1983 (V. H. Ruiz, in litt., 21 October 1989). Photographs of the skeleton, kindly provided by V. H. Ruiz, demonstrate that the specimen was not physically mature.

15. An adult right whale dolphin stranded on the beach of Burca (36° 28′S, 72° 55′W) in 1984 was examined for parasites (Fernandez 1987). No other information is available.

16. A complete skull of a physically mature animal was collected by Henry Camera on the beach of Matanzas (33° 58′S, 71° 55′W), in February 1986. The skull is deposited at the laboratory for marine mammals, Museo Nacional de Historia Natural (MNHN), Santiago.

17. A slightly damaged calvarium of an adult dolphin was picked up from the beach of Cachinales (25° 10′S) by C. Guerra in July 1986 and was identified by the senior author. It is kept at the Instituto de Investigaciones Oceanológicas of the University of Antofagasta, under no. AMM-019 (C. Guerra, unpublished data).

18. and 19. Between 16 and 28 August 1986, observations of cetaceans were made off northern Chile by KVW on board the high sea purse-seiner Guanaye operating out of Mejillones. On the six cruises total observation time was 57 hours 55 minutes in the area 22° to 24°S and the coast to 150 km offshore (see van Waerebeek and Guerra 1987). On 27 August 1986 (08:30 h) at 23° 46′S, 71° 25′W some 200 right whale dolphins were observed travelling north at high speed, accompanied by a small number of common dolphins (*Delphinus delphis*) and seabirds. Video and still photographs were taken. Later the same day (11:20 h), at 23° 31′S, 71° 00′W, a very dispersed herd of 30–50 right whale dolphins, also going north, was photographed. The dolphins changed direction upon approach (van Waerebeek and Guerra 1987).

20. and 21. The captain of the Guanaye, Enrique Garcia, made video recordings of two groups of right whale dolphins off northern Chile (Antofagasta) as follows: 20–30 specimens at 23° 30′S, 71° 02′W on 30 August 1986; and 200–250 animals at 24° 00′S, 70° 50′W on 29 August 1986. The identifications were confirmed by the senior author (in Guerra et al. 1987).

22. On 23 November 1987, Juan C. Torres found the carcass of a young right whale dolphin on a beach of Isla Guafo, a small island south of Chiloé (43° 37′S, 74° 40′W). The difficult access to the beach permitted him to collect only the calvarium, which is at the Museo Nacional de Historia Natural, Santiago (MNHN 1155).

23. A 218 cm, pregnant female in fresh condition, stranded on the beach of Mehuín (39° 26′S) on 11 November 1987. No signs of a fishery interaction could be discerned on the carcass. J. A. Oporto collected and deep-froze the specimen (JAO–041) for further study at CIMMA, Universidad Austral de Chile, Valdivia. Preliminary results of the necropsy are discussed by van Waerebeek and Oporto (1990).

24. On 27 June 1988, JGV found a 261 cm male right whale dolphin stranded relatively fresh near the mouth of the Copiapó river (27° 20′S, 71° 00′W). Photographs were deposited at MNHN (Santiago), but it was not possible to save the carcass.

25. On 21 July 1988, a 198 cm female was accidentally captured in a gill net some 20 nautical miles off Matarani (16° 57′S) in southern Peru (Lazarte and Valdivia 1988). The skull is at the Instituto de Investigación y Desarrollo Hidrobiológico of Catarindo (Mollendo). This was the first record of the right whale dolphin for Peruvian waters.

26. A group of about 400 southern right whale dolphins was photographed by Jack Grove (pers. comm.) on 16 November 1988 at 33° 03′S, 72° 33′W on board the M. V. Society Explorer. When encountered, the dolphins were heading south and apparently were feeding on densely schooling fish, as judged from the prey's jumping behaviour. No calves were seen, but common dolphins were mixed in the main group (Jefferson et al. 1991). The water temperature was 14 °C, water depth 5,000 m.

27. A 250.5 cm sexually mature male was landed by artisanal fishermen at Pucusana (12° 30′S), central Peru, on 15 November 1989. The specimen had drowned only hours earlier in a drift gill net. Skeletal and soft tissues were sampled by the senior author and included in the CEPEC collection (KVW-1857). Information on its stomach contents and parasites are reported in van Waerebeek and Oporto (1990). The exact catch locality is unknown; however, local fishermen are known to operate usually well within 60–100 km of port. This record, the second for Peru, extends the known range of the species 5° north in the Southeast Pacific and the world. One fisherman, regarded as a reliable source, claimed that another specimen of this species had been brought into the port of Callao (12° 03°S), Peru, a month earlier. However, without proof the latter report must be classified as "unconfirmed".

28. A disarticulated but complete skeleton of an animal of unknown sex was collected from Playa Mamani (29° 03′S), north of Coquimbo, in late January 1990 (J. Gibbons, pers. comm.).

29. J. Gonzalez found a posterior tail stock and flukes (span: 36.5 cm) of a specimen

on the beach of Carrizal Bajo (28° 05′ S), relatively fresh, in the summer of 1990. From cut marks it was evident that the tail had been severed by fishermen. Identification was based on the contrasting black/white pattern on both sides of the flukes, and the shape of the latter. The specimen and two photographs are at MNHN (Santiago).

30. An adult male of unkown length was caught in a drift gill net set some 90 nautical miles west of San Antonio (33° 35′ S), for swordfish (*Xiphias gladius*), on 8 July 1990. Meat of the animal was consumed by the fishermen. One of us (JLB) took photographs and saved the skull, which are kept as voucher material at the Museo Municipal de San Antonio (MMSA-CE-12). Reyes and Brito (1990) describe trematodes, *Nasitrema* sp., from the cranial sinuses; these same trematodes also had been found in the first specimen from central Peru (van Waerebeek and Oporto 1990).

31. On 17 August 1990 the remains of a male, measuring a minimum of 230 cm (the tail was missing), were found on a beach close to the artisanal fish terminal of San Antonio, Chile. The dorsal musculature had been removed for human consumption. It was learned that the animal had been caught 120 nautical miles west of Quintero (32° 46′ S) in a gill net set for swordfish. The stomach contents included unidentified otoliths and remains of cephalopods and decapod crustaceans. The skeleton and other biological material are at the collection of the Museo Municipal de San Antonio (MMSA-CE-13).

32. A 271 cm, sexually mature male was caught in a gill net and landed by artisanal fishermen at the Pucusana fish terminal, central Peru, on 8 September 1990. Soft tissues and skeleton, collected by J. C. Reyes and M.-F. van Bressem, were incorporated in the CEPEC collection under number JCR-1800 (Reyes, pers. comm.).

33. The complete carcass of a male (length unknown), in an early state of decomposition, was found by Jaime Lama on the beach of Punto Viejo (27° 21′ S) on 19 September 1990. It was noted that several dead Humboldt penguins (*Spheniscus humboldtii*) had also washed up in the vicinity, suggesting all were killed in a gill net fishery. The specimen was lost, but a voucher photograph is at MNHN, Santiago.

34. J. Capella and Y. Vilina examined the remains of a 297 cm male stranded on the beach of Caleta Chañaral (26° 21′ S), during the first week of October 1990. No material was collected, but photographs were deposited in the files of the National Museum in Santiago.

35. On 3 February 1990, observers aboard the M/S World Discoverer encountered a large herd (ca. 800–1200 animals) in 360 m of water southwest of Peninsula Taitao, Aisén (46° 12′ S, 74° 29′ W). Several small groups of right whale dolphins were traveling on the perimeter of the herd and came to the bow of the vessel to ride its bow wave. At least two very small calves were present (S. Leatherwood, in litt. June 1991).

36. Claudio Rivera, captain of the purse seiner Kofuko-Maru, observed a large group (ca. 1000 animals) of right whale dolphins, 70–80 nautical miles offshore between San Antonio (33° 35′ S) and Pichilemu (34° 24′ S) in Juni 1983. The animals were heading east. Photographs are deposited at the Museo Municipal de San Antonio.

Discussion

Misidentifications

Based on an account by Reed (1904), Donoso-Barros (1975), cited in Sielfeld (1983), refers to the Bay of Concepción (± 37°S) as a record locality for right whale dolphins. A careful reading of Reed's paper, however, reveals that the dolphin in question had a 12 cm high dorsal fin; the specimen has been correctly reidentified by Goodall et al. (1988) as a Chilean dolphin, *Cephalorhynchus eutropia*.

Another skull believed to have originated from Concepción, Chile (Cruickshank and Brown 1981), but with no other data than a label with “Baie de la Conception“, is at the

Paris Museum d'Histoire Naturelle (MNHN-1928.195). However, as the aforementioned authors admit, that specimen may have been collected at Conception Bay, Namibia (23° 55′S, 14° 13′E). New evidence from FINDLAY (1989) and ROSE and PAYNE (1991), who identified the area as a concentration zone for right whale dolphins, lends substantial support to this possibility. Until more information becomes available we classify this skull as incertae sedis.

The type specimen of *Tursio chiloensis* Philippi, 1900 based on a calvarium from Ancud (41° 53′S, 73° 48′W), Chiloé, was long put into synonymy with *L. peronii* (HERSHKOVITZ 1966; DONOSO-BARROS 1975; SIELFELD 1983). Our own observations on the specimen, at the Santiago Natural History Museum, are in agreement with GOODALL (1986), who reassigned it to Peale's dolphin (*Lagenorhynchus australis*).

Abundance

There are no world population estimates available, nor have separate stocks been described (JEFFERSON and LEATHERWOOD 1990). The abundance of right whale dolphins off Chile has been characterized from "very rare" (YAÑEZ 1948) to "common along the entire coastline [of the Province of Concepción]" (OLIVER-SCHNEIDER 1946). Also they have been reported to occur with some regularity off southern South America, especially around Cape Horn (BENNETT 1840; D'ORBIGNY and GERVAIS 1847; BROWNELL 1974). During shipboard surveys off northern Chile in August 1986, right whale dolphins were the second most commonly observed cetacean after the dusky dolphin, *Lagenorhynchus obscurus* (VAN WAEREBEEK and GUERRA 1987; see sightings # 18–21). Mean group size during these and other observations in the study region was 368 (SE = 111; range 20–1,000; N = 10). Also, the rapid accumulation of new stranding records in recent years, admittedly thanks to increased research effort, indicates that right whale dolphins are not rare in the region. However, studies to assess absolute population densities have not been made and even approximate estimates can not be given. The need for such research is urgent since recent data suggest a considerable and possibly increasing fishery mortality. The rapid development of a swordfish gill net fishery off central Chile is particularly alarming (REYES and OPORTO 1990).

Habitat

Southern right whale dolphins are typically pelagic and found close to shore only in deep water (BROWNELL 1974; JEFFERSON and LEATHERWOOD 1990). The confusion about AGUAYO's (1975) characterization of this species off Chile as "pelagic and coastal" (see: LEATHERWOOD and REEVES 1983; CRUICKSHANK and BROWN 1981) is in our opinion but a semantic one. At the sites where southern right whale dolphins were seen inshore ("coastal"), the continental shelf is very narrow and the habitat oceanic, which is the case for most of the Chilean coast north of Valparaiso. Similarly, after examining several so-called "inshore" sightings in the Southeast Atlantic and southern Indian Oceans, CRUICKSHANK and BROWN (1981) concluded that *L. peronii* should be considered a deep-water species.

GOODALL (1978, 1989) believes that right whale dolphins may occasionally enter shallow waters; she has found beached specimens, though none fresh, in the channels of Tierra del Fuego. We are not aware of any sightings to confirm this contention.

During the 672 observation hours and 2,597 nautical miles of a boat survey for cetaceans through the channels between Puerto Montt and Punta Arenas (Regions Aisén and Magallanes), 29 sightings were made of six small cetacean species, but none of the right whale dolphin (OPORTO 1984). Several other boat and aerial surveys in the region (SIELFELD and VENEGAS 1978; LEATHERWOOD et al. 1988) and extensive shipboard surveying in shelf-water (less than 200 m) around Chiloé, off western Magallanes and in

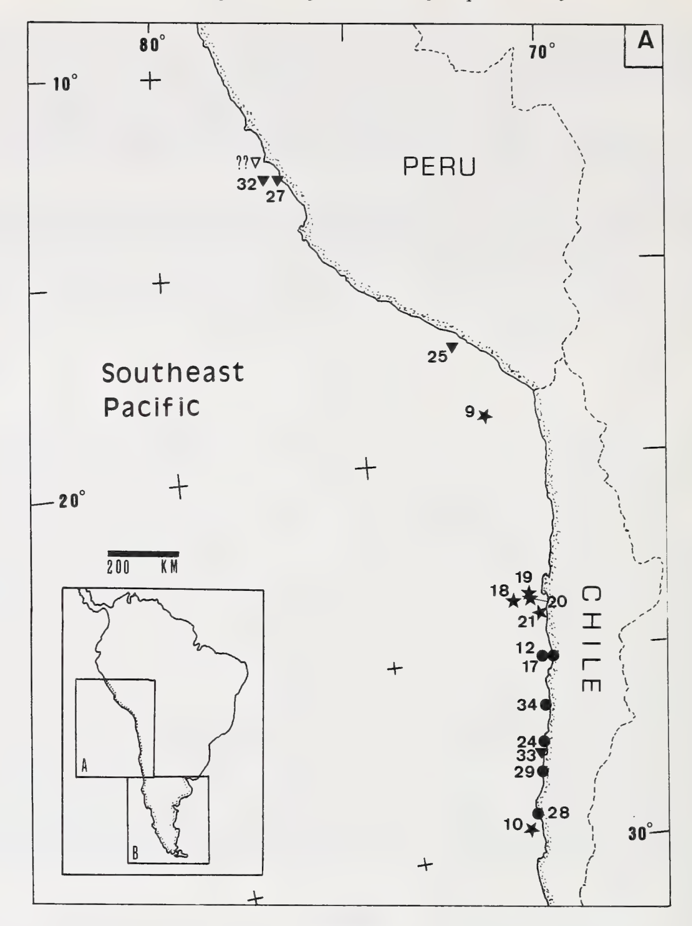


Fig. 1A

the Strait of Magellan (A. C. Lescrauwaet, pers. comm.) neither yielded a single sighting of right whale dolphin. The absence of right whale dolphins among the remains of eight small cetacean species discovered in an archaeological site near Ushuaia (54° 47′S, 68° 20′W), on the northern shore of the Beagle Channel (Piana et al. 1986), further reinforces our feeling that under normal circumstances this species avoids shallow water. Probably individuals enter Fuegian channels only accidentally or when unhealthy; these are likely to strand due to the unfamiliar environment, which in turn could help explain the skeletal material found by Goodall (1989).

The three published specimen records of right whale dolphins registered from Chilean Magallanes originated from Bahías Posesión and Lomas at the eastern entrance of the Strait of Magellan (Venegas and Sielfeld 1978; Sielfeld 1983). Based on geographical considerations, there is little doubt that the specimens came from the Southwest Atlantic, which falls outside the scope of the present paper.

Seasonal movements

So far migrations or seasonal movements have not been described for this species (Jefferson and Leatherwood 1990). The seasonality of sightings, captures and strand-

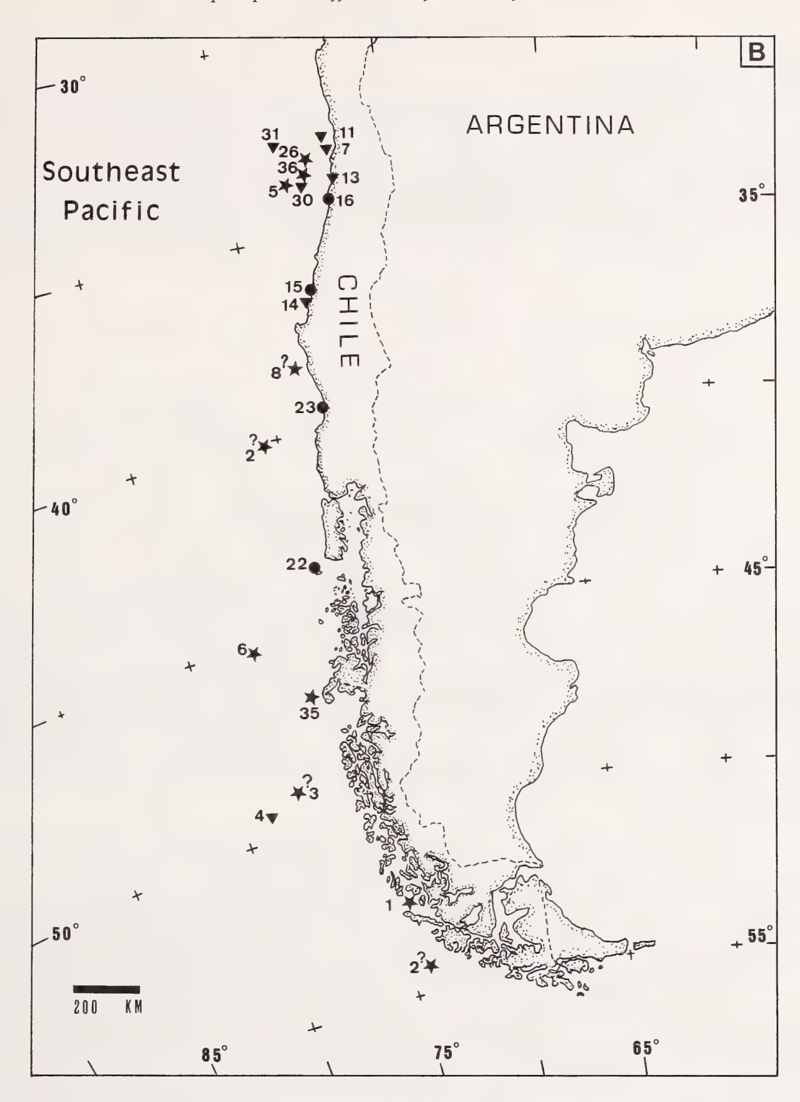


Fig. 1. Distribution of southern right whale dolphin off the coasts of Peru [A] and Chile [A, B], as indicated by documented records from 1823–1990 including sightings (★), animals caught in fishing gear (▼) and stranded specimens (●). Numbers concur with these in the list of records. A question mark indicates that the location of the record is only approximately known; a double question mark represents an unconfirmed record

ings of fresh specimens off the Pacific coast of South America (n = 24) is shown in Fig. 2. Although the sample size is small, significantly more records were registered north of 25°S in July–September than in all other months combined (chi-square, $p < 0.05$, $N = 8$). This suggests that at least part of the Chilean population may undertake a northbound migration in the austral winter and spring when cool coastal upwelling and the coastal component of the cold Humboldt Current (Fiords Current) are strongest (Bernal et al. 1982; Brink et al. 1983). Five of the six specimens examined from north of 30°S were

males; however, more data will be needed to determine whether males are more likely to move into northern waters.

Between 25° and 40°S off the Chilean coast, right whale dolphins are present year-round. Sightings made south of 40°S are limited to summer months, which we believe is related more to observer's seasonality than to dolphin's occurrence.

Year-round boat or aerial surveys will be needed to clearly establish seasonal movements. If firm evidence of migration becomes available, it will bear implications for the species' conservation, calling for management measures on a regional rather than national level.

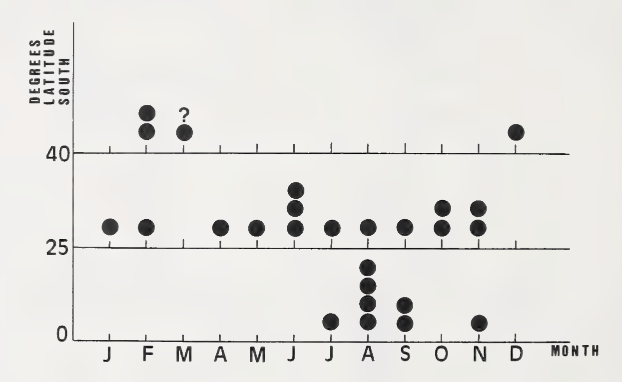


Fig. 2. Monthly pattern of confirmed sightings and records of captured and freshly stranded specimens of southern right whale dolphin, in function of latitude (in degrees) along the Pacific coast of South America. Note the concentration of records in austral winter and spring at low latitudes. Late summer record (# 1) from Lesson and Garnot (1826) is assumed to have occurred in March and is indicated by a question mark

Distribution centres and boundaries

The occurrence of small cetaceans off Peru was intensively studied in the period 1985–1990 through monitoring of cetacean landings at fishing ports and surveying of beaches and fish dumps (Read et al. 1987; van Waerebeek et al. 1988; van Waerebeek and Reyes 1990). Until today, only three southern right whale dolphins are known from Peru, two of these encountered at Pucusana (# 27, # 32). The latter, from 12° 30′S, represent the most northern records of southern right whale dolphin in the SE Pacific and worldwide.

It is not yet clear whether right whale dolphins are more than an occasional winter visitor to central Peruvian waters. Both Pucusana specimens, although heavily parasitized, seemed to be in good health; otoliths in the stomach of one (# 27) indicated that it had been feeding extensively on anchoveta (van Waerebeek and Oporto 1990).

All sightings north of 40°S lie within a strip ca 170 km from shore. It is reasonable to expect that the western distribution barrier is formed by the rapidly increasing temperatures of the eastern subtropical Pacific, beyond the cold waters of the Humboldt Current 300–400 km offshore (Bernal et al. 1982). Off southern Chile right whale dolphins have been seen up to 250 km offshore where their distribution broaden to merge with the subantarctic waters of the circumpolar West Wind Drift. The southern boundary south of Cape Horn is currently set at ca 57°S (Drake Passage) where a small group was sighted by Kasamatsu et al. (1990).

Data do not yet permit one to identify distribution centre(s) because of the highly uneven observer effort in different areas. The apparent concentration of records around Antofagasta and off Valparaíso doubtless reflects a higher density of observers.

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Zusammenfassung

Das Vorkommen des südlichen Glattdelphins Lissodelphis peronii vor der Pazifik-Küste von Südamerika

Verbreitung und Zugverhalten des südlichen Glattdelphins (*Lissodelphis peronii*) wurden vor der Westküste Südamerikas erforscht. Angegeben werden eine chronologische Liste und eine Karte von 36 bestätigten Beobachtungen zwischen 1823 und 1990, von denen fast die Hälfte bisher unveröffentlicht waren. Die Beobachtungen aus Beifang, Strandungen und Sichtungen wurden nur als gültig angesehen, wenn verbürgtes Material vorlag. Eine erste Durchsicht des Daten zeigt, daß *L. peronii* zu den häufigsten Cetaceen vor der nordchilenischen Küste gehören könnte. Die durchschnittliche Größe der Schulen beträgt 368 Exemplare. Allerdings nimmt das Verfangen in Netzen alarmierend zu. Abschätzungen über Populationsdichte und Mortalität durch Fischerei sind dringend nötig. Das normale Habitat von *L. peronii* vor Südamerika scheint streng pelagisch. Zwei bei Pucusana (12° 30′ S) gefangene Exemplare erweitern die bisher bekannte Verbreitung um 5° nach Norden und stellen für Peru die zweite und dritte Beobachtung dar. Nördlich von 25° S wurden von Juli bis September mehr Beobachtungen gemacht als in allen anderen Monaten zusammen, was ein Ausweichen nach Norden im Südwinter/Frühjahr nahelegt. Vor Chile kommt *L. peronii* zwischen 25° S und 40° S ganzjährig vor. Die gegenwärtigen Westgrenzen der Verbreitung liegen nördlich von 40° S 170 km vom Festland und 250 km vor der südchilenischen Küste. Im Bereich der Westwindzonen gehen sie in eine zirkumpolare Verbreitung über.

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Population ecology of the Hairy-footed gerbil, *Gerbillurus paeba*, in a coastal dunefield of South Africa

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Abstract

Studied was a population of the hairy-footed gerbil, *Gerbillurus paeba*, in the Alexandria dunefield along the eastern Cape coast, South Africa, from March 1981 to July 1982. *G. paeba* is the only resident rodent species and is endemic to this dunefield. A mark multiple-recapture study showed that the gerbil density was low, averaging 1,7 gerbils/ha. Annual population turnover occurred, with highest and lowest numbers being found in late summer and late winter, respectively.

Introduction

The species *Gerbillurus paeba* Smith, 1836, contains four subspecies of "hairy-footed gerbils" typical of arid sandy habitats in southern Africa. Of these, *Gerbillurus paeba exilis* Shortridge & Carter, 1938, is unique in being recorded from only a single coastal sand dunefield. It thus warrants special conservation status for which knowledge of its population biology would be useful.

The most widely used method for obtaining data on the population dynamics of small mammal populations is mark-recapture census coupled to a population model which yields estimates of population numbers and gain and loss rates. This method was used to investigate the population ecology of the hairy-footed gerbil *G. p. exilis* in coastal dunes.

Material and methods

Study area

The Alexandria dunefield, lining the northern shores of Algoa Bay, is the largest active coastal dune system in South Africa. The major part of the dunefield lies between the mouth of the Sundays River (33° 44′ S; 25° 51′ E) and Cape Padrone, 48 km to the east. The climate is warm temperate, but variable. Rain may occur in all months of the year and averages 400–800 mm p.a. along the dunefield from W to E. Mean annual temperature for the study period (1981 and 1982) was 17.7 °C. Lowest and highest temperatures recorded were 3.9 and 40.0 °C, respectively.

The dunefield includes a series of 36 damp hollows (slacks) separated by bare dune ridges, extending in a strip 3.5 km long, parallel to the shoreline. Five slacks were covered by the live trap grid. Each slack is approximately 200 m long and 40–50 m wide. Due to the action of the predominantly west winds, the slacks migrate eastwards at a rate of 7 m per year. To the south, they are bordered by the beach, to the north, by high dunes (McLachlan et al. 1987) (Fig. 1).

Vegetation in the slacks is sparse, averaging 2–10 % cover and rarely exceeds 0.5 m in height. Most abundant plants are two hummock forming species, *Arctotheca populifolia* and *Gazania rigens*, and sandgrass, *Sporobolus virginicus*. *G. p. exilis* is the only rodent permanently resident in the slacks.

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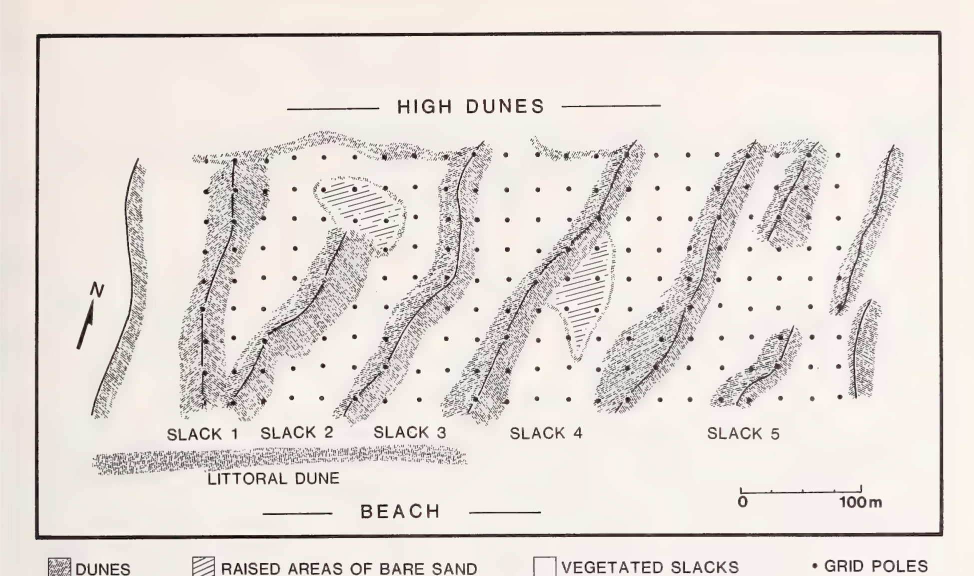


Fig. 1. The study grid

Trapping procedure

A mark multiple-recapture programme was carried out from March 1981 to July 1982 at three-weekly intervals. A fixed grid was laid out over six dunes and their five corresponding slacks, chosen as being typical of the area. The grid covered the entire length of the slacks, since a pilot study indicated that the slacks were the chief habitat of the gerbils. The grid dimensions were 525 m × 200 m (area: 10.5 ha), with the long axis lying parallel to the beach (see Fig. 1): 198 poles were placed 25 m apart in 9 rows of 22 lines. Approximately half the stations were situated on dune slopes, the remainder in slacks. Each trapping session lasted 48 h. On trap night one, all traps were moved 25 m and reset at the previously vacant stations. The two trap nights comprised one trapping session, the data from the two nights being pooled.

Every alternate trapping session the sampling was extended to last three nights. On the third night 40 traps were placed in a square outside of the grid (10 traps per side). The distance of this square from the outermost stations of the grid varied from 50 m to 200 m, averaging 100 m. The additional information obtained from these traps was used to estimate population density more accurately by quantifying immigration and emigration, and in analysis of home ranges of individuals.

Small Sherman aluminium live-traps, baited with a mixture of rolled oats and water, were set in the late afternoon and checked the following morning. Each trap was set with its entrance opposite the prevailing wind. During very windy or rainy weather each trap was covered with a plastic bag, to provide cover. Squares of loosely woven material were provided as thermal insulation. Each newly-captured gerbil was individually marked using an ear-clipping technique, identified, weighed to the nearest 0.5 g, sexed, and its reproductive condition recorded. Males were classified as having scrotal or abdominal testes, while females were classified according to nipple size [medium or large (Krebs 1966)] and pregnancy. The location of each capture was noted and the gerbils released at the point of capture.

Analysis of data : trapping success, trap efficiency and trappability of the population

Nelson and Clark (1973) have stressed the need to account for decreases in trapping efficiency resulting from traps being rendered ineffective, and suggest a correction factor. It is assumed that, on average, each sprung trap is ineffectual for half the trapping interval. The percentage trapping success has been calculated as:

$$\% \text{ trapping success} = \frac{A \times 100}{N - S/2}, \text{ where A = no. of animals captured;}$$

N = no. traps; S = total no. of traps sprung by mice or nonfunctional.

Percentage trap efficiency is calculated as:

$$\% \text{ trap efficiency} = \frac{(N - S/2) \times 100}{N}$$

Trap efficiency was only quantified from the fourth sample onwards.
Trappability of the population (Krebs et al. 1969) was estimated as:

$$T = \frac{\text{no. caught at time t} \times 100}{\text{no. known to be alive at time t}}$$

Sex ratio

Chi-square tests, incorporating Yates' correction for continuity (Zar 1984), were used to determine whether the sex ratio deviated from parity.

Age structure

Since the only reliable age determination criteria (e.g. eye lens weights) are obtained from dead animals (Morris 1972), no absolute age classes could be established. It was felt that no animals in the dune area should be snap-trapped, since the total area of suitable habitat is small, and population numbers were low. Although body weight is not a good criterion of age, since it is influenced by, inter alia, diet and season (Pucek and Lowe 1975), it has been used as an approximate indicator of age (Krebs 1966; Tamarin 1977; Perrin 1979; Montgomery 1980) and is easily measured in the field (Ford 1981). The study population was divided into two classes, juveniles and adults, on the basis of weight (and sexual maturity). Juveniles were defined as those animals having a mass of $\leq$ 26 g. The males had abdominal testes and the females had very small, undeveloped nipples, characteristic of females that had never produced a litter.

Population size, recruitment, losses

Population size was estimated using the direct enumeration method of Krebs (1966).

Minimum Number Alive (MNA) at time t = actual no. caught to time t + no. of previously marked individuals caught after time t, but not at that time.

This method has been used frequently: Tamarin 1977; Perrin 1979; Christian 1979, 1980; Chidumayo 1980. Cheeseman and Delany (1979) compared the results obtained from five methods of population assessments for rodents in tropical African grassland and concluded that the direct enumeration method was the most satisfactory.

Survival rates were calculated after the method of Krebs (1966): minimum survival rate (S)

$$= \frac{\text{no. of individuals known to be alive at time t + x}}{\text{no. known to be alive at t}}$$

where t = time and x is the interval between sampling occasions. 1 − S = population loss (emigration + mortality). Student's t-test (Zar 1984) was used to test for differences between summer and winter survival rates.

Population density

Estimating population density, by dividing the population number by the area of the grid, usually results in an overestimate of density, since the effective sampling area (from which mice move to traps) is actually larger that the grid (Smith et al. 1975). An attempt was made to reduce this bias by adding a boundary strip to the area of the grid, the width of which represents the average distance moved between successive captures (Brant 1962). The boundary strip was added to the eastern and western sides of the grid, since only these sides were bordered by suitable habitat. Population density was estimated by dividing the MNA population estimate by: 10.5 ha (grid area) + 4.0 ha (boundary strip) = 14.5 ha.

Results and discussion

General trapping results

138 gerbils were captured 725 times during the study. There was a marked seasonal change in numbers (Fig. 2), with lowest numbers occurring in late winter and peak numbers in late summer, following the onset of the breeding season. Trapping success averaged 23 %,

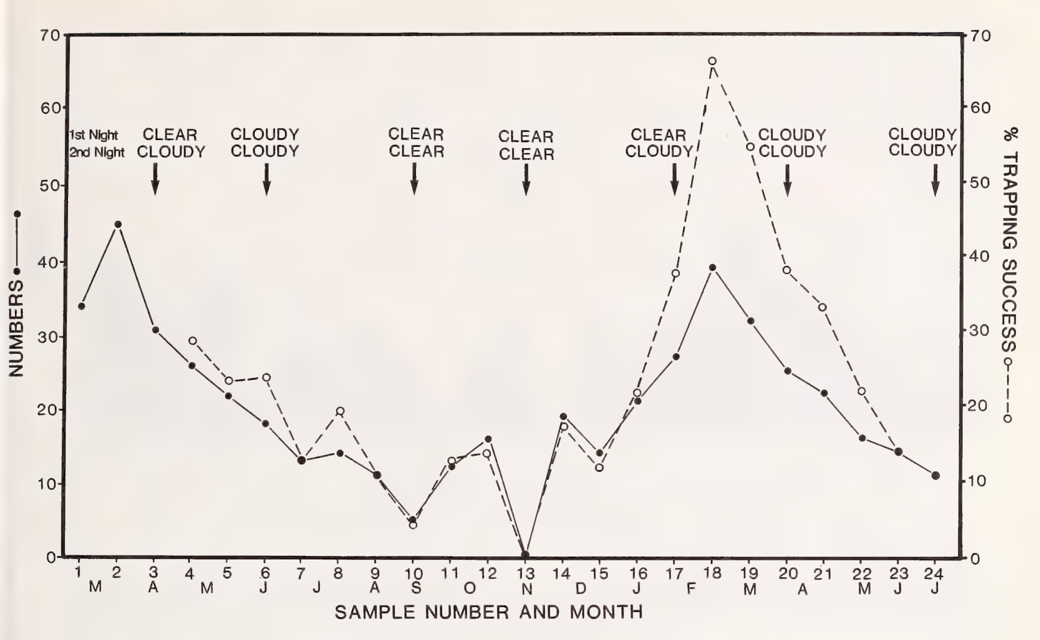


Fig. 2. Numbers of *G. p. exilis* caught from March 1981 to July 1982. Arrows and annotations indicate sample near full moon and cloud cover. Broken line indicates percent trapping success

dropping to 0 % in November and peaking at 67 % in February (Fig. 2). Numbers of gerbils captured was low, despite the use of a large grid. The low capture rate is not due to a faulty trapping procedure. SMITH (1968) has stated that the probability of an animal being caught in a trap is the product of: 1. the probability of the animal encountering a trap, 2. the efficiency of the trap and 3. the response of the animal to the trap. With regard to (1), the large distance moved by the gerbils reduces the probability of large trap spacing causing of small sample sizes; many gerbils were caught at several hundred meter intervals on successive nights. SOUTHERN (1973) warns that sufficient traps must be available for all potential captives: in the present study, no more that 33 % of the traps were full on any occasion.

Trap efficiency (2) was quantified regularly, each trap being checked each morning. The major causes of non-functioning traps were clogging by sand in windy conditions (24 %) and traps sprung either by the wind or by isopods *(Tylos capensis)* or earwigs *(Labidura riparia)*. The unstable substrate and sparseness of vegetative cover caused sampling errors: although traps were covered with plastic bags in unfavorable weather to minimise the amount of sand entering through joints, and placed with their entrances away from the prevailing wind, the wind often changed direction (unpredictably) during the night and traps facing into strong wind filled with sand within minutes. Despite these difficulties, trap efficiency never fell below 59 %, and averaged 69 %. Trap efficiency is unlikely to have biased sampling results significantly. This leaves only the response of animals to the traps as a possible cause of small samples. Since both adults and juveniles, males and females, were captured, recapture numbers were high and the average trappability of the population was 79 %, it seems unlikely that any part of the population was permanently untrappable. A variable response by individuals, or differences between animals of different social rank might be implicated.

More mice in a population may be caught if each sampling period is extended (SMITH 1968). Sampling for more than two days per sampling trip was logistically impossible in the

present study. However, results obtained from 11 sampling occasions when traps were set for a third night, show that a further 6 % of marked individuals were caught on the third night that were not captured on one of the previous two nights. Unmarked gerbils caught on the third night are assumed to have been drawn from outside the study grid. Two trap nights therefore appear to be adequate for enumeration of the study grid population. Since less than half the grid area comprised suitable habitat, it might be realistic to express the effective grid as 5.25 ha, rather than as 10.5 ha, thereby doubling density.

Sampling number 13 (November 1981) was omitted from the results, because only one gerbil was caught during the entire 48 hours sample. The minimum number known to be alive was 12. The percentage of gerbils recaptured was high, averaging 80 % for the study period, excluding the first two samples, since the marking programme was just beginning, as well as sample 13. The lower number of recaptures in August and October (samples 8, 9, 11, 12) was due to the appearance on the grid of new, adult, mostly male mice, presumably to occupy gaps in the area left by gerbils that had died during the winter, and also to breed. From early December onwards (samples 14–18) the smaller number of recaptures was due to the appearance of new, juvenile mice from the spring-summer breeding period as well as new, older individuals (Ascaray 1986). The recapture rates of males and females were similar. Slightly higher recapture rates of females from March-June 1981 and males from February-May 1982 can be attributed to the higher numbers of females and males, respectively, during those periods. The high recapture rate tends to support the conclusion that the low numbers captured indicate a small population and are not a sampling artefact.

Population structure

Sex Ratio

Of the 138 gerbils marked, 67 were male and 71 were female, giving a sex ratio of 1 male : 1.06 females. This does not differ significantly from a 1 : 1 ratio (chi-squared; $p > 0.05$). Since male *G. p. exilis* move larger distances than females during the breeding season (Ascaray 1986), there may in fact be a lower proportion of males than the sex ratio suggests.

The number of females caught was consistently lower than the number of males, except for April and May 1981. Since numbers from individual samples were mostly too small to perform valid statistical tests, the data were grouped and tested for seasonal differences. There was not significant deviation from a 1 : 1 sex ratio in any one season (Chi-squared; $p > 0.05$).

Age structure

The age structure of *G. p exilis* over 17 months (Fig. 3) indicates a population of seasonal breeders, since juveniles are produced in cohorts at fixed intervals.

There were no juveniles present in the population from July 1981 to early October 1981 since all juveniles from the previous breeding season had reached maturity by July 1981. They overwintered as adults and began breeding in September. Appearance of juveniles in the population was delayed until the end of October, when those conceived at the beginning of the season had been weaned and were emerging from nests to become part of the trappable population. The number of juveniles began to decrease at the end of the breeding season as they matured. All juveniles reached adulthood by the end of June 1982.

The number of adults decreased following the end of the breeding season, despite the recruitment of maturing juveniles. This appears to have been due to the death of the adults born in the previous breeding season. Of 71 gerbils, only three individuals (4 %) were known to have survived one year. The longest-lived gerbil survived 13 months. *G. p. exilis* exhibits annual population turnover, i.e. juveniles from one breeding season do not survive beyond the next breeding season.

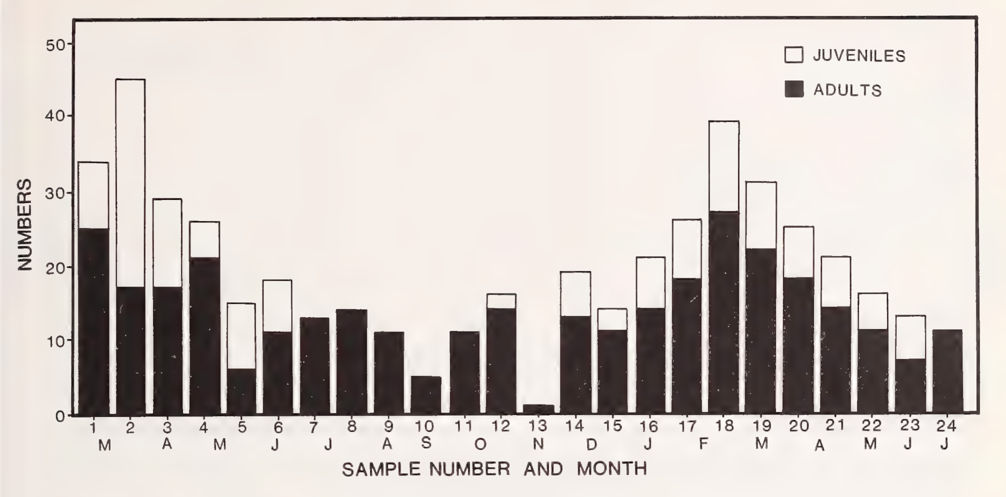


Fig. 3. Age structure of *G. p. exilis*

The unusually large number of juveniles captured directly after the flood on March 1981 may have been trapped on the grid by the water. They had died or emigrated from the area before the following trapping occasion.

Population dynamics

Population size

The MNA gave population estimates 24 % higher than the numbers trapped (Fig. 4). Bishop and Sheppard (1973) have found that the population estimate is usually reliable when 9 % or more of a population is sampled, and the survival rate is not less than 0.5; both these conditions were fulfilled. Hilborn et al. (1976) noted in simulation studies that the MNA is generally 10–20 % below population size.

Peak numbers (MNA = 48) occurred in February-April, while numbers reached their lowest just after the winter months, in later August and September (MNA = 10). This fluctuation was caused largely by the seasonal breeding pattern. The breeding period gave rise to high numbers in late summer, which, because of increased mortality during winter and very little further recruitment, declined to a low before the start of the next breeding season. Christian (1979, 1980) found that *G. p. paeba* in the Namib Desert reached peak numbers in September-October and then declined. Boyer (1987) recorded reproduction and recruitment of *G. tytonis* in summer in the Namib. This seasonal pattern is the converse of the pattern occurring in the Alexandria dunefield. In the Namib Desert, the timing of reproductive season is controlled by rainfall and there is a pronounced decline in breeding activity during the hot dry portions of the year (Christian 1980). Nel (1983) reports that *G. paeba* reaches peak numbers in July in the Kalahari Gemsbok National Park, with lowest numbers occurring in December. Similarly, this cycle appears to be adapted to the rainy season, which extends from November to April, peaking in January-March, depending on location (Nel and Rautenbach 1975). Water is not a limiting factor in the Alexandria dunefield (Ascaray 1986) and the breeding period of *G. p. exilis* appears to be controlled by plant production rather than by rainfall per se.

Marked fluctuations in density over several years are common in desert rodents. These fluctuations are caused by a variation in reproductive activity, which depends on plant production, and thus ultimately on the highly erratic rainfall such regions receive (Christ-

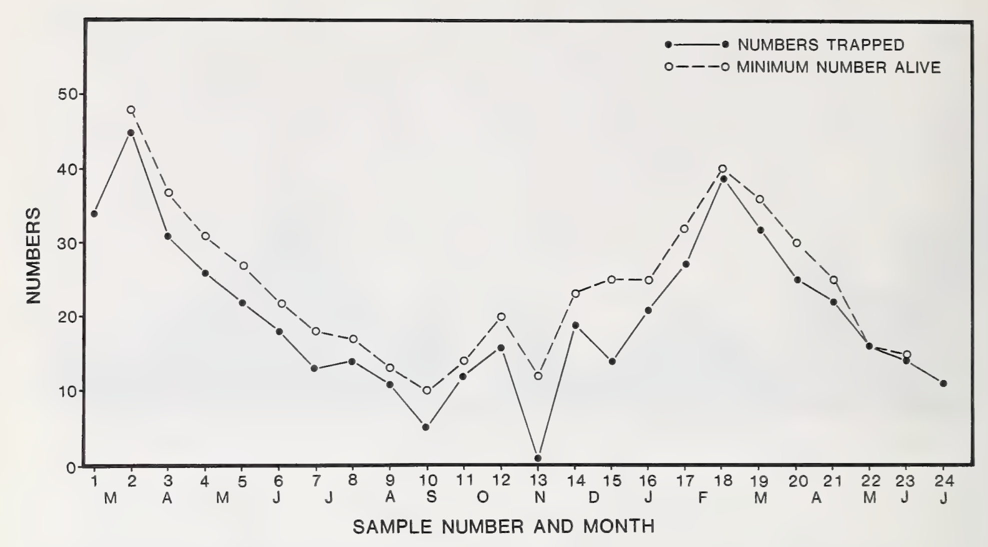


Fig. 4. Two estimates of population size of *G. p. exilis*

IAN 1980). NEL (1983) demonstrated large population fluctuations of *G. p. paeba* in two different habitats over several years in the Kalahari Gemsbok National Park. No long term data are available for *G. p. exilis.*

Population losses

A decrease in population size may be due to emigration and/or mortality: they are often quantified together as population loss. Population loss can only be estimated for the trappable population; neonatal mortality is excluded. Results may be expressed as survival rates, where survival = 1 – population loss (thereby introducing an error). Survival estimates, based on MNA are shown in Fig. 5. It is preferable to calculate survival of adults and juveniles, males and females, separately, since each class may suffer differential mortality. CHRISTIAN (1980), for example, found that male *G. p. paeba* in the Namib Desert have a significantly higher survival rate than females. The two estimates for the dune slack populations are very similar, the average being 4 %.

According to KREBS (1966), estimates of survival are accurate when recapture rates are high, as in the present study. Survival between samples, averaged 0.80 for the study period. CHRISTIAN (1979) found a similar mean rate of ≥ 0.84 for Namib Desert populations. Survival was significantly lower in winter than in summer ($p < 0.05$) in the dune slacks. Possible reasons are colder temperatures and decreased food availability. The combination of low temperatures and protracted rainy weather when burrows become completely saturated, may be particularly unfavorable to the gerbils.

The seasonal increase in population size appears to have two causes: and increase in survival rate as well as the influx of new individuals.

The March 1981 floods appeared to affect survival, since the survival rate dropped from 0.74 to 0.66 following the flood. Juveniles were most affected.

Predators which visit the dune slacks include jackals, genets and owls. Jackal tracks indicated that gerbils were taken by jackals. LAYCOCK (1975) reported that several gerbils were removed from traps by jackals in the Namib Desert. One gerbil was taken by a genet on the slip-face during the pilot study (ASCARAY 1980) and genet tracks were regularly observed in the dune slacks. *G. paeba* skulls have been found in barn owl pellets near the dunefield (ASCARAY 1980).

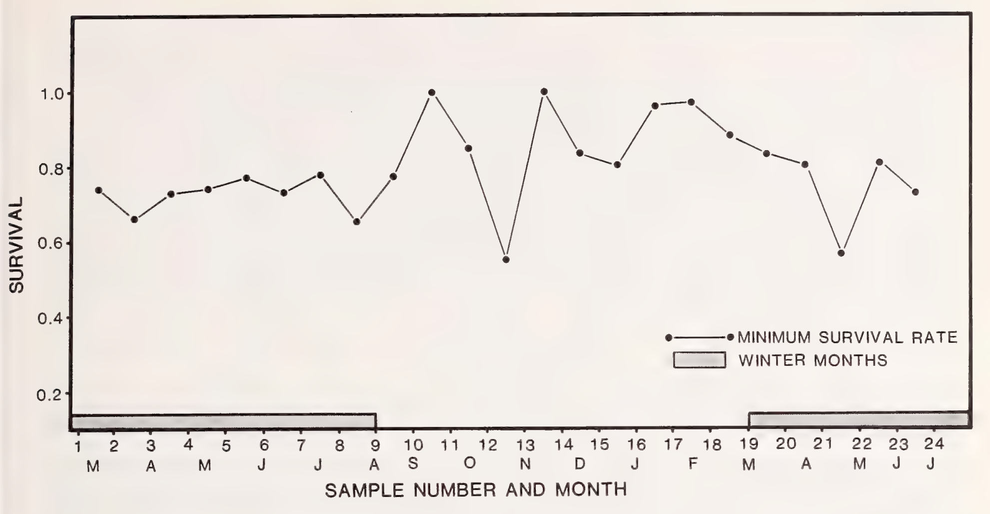


Fig. 5. Survival rate (per 3 weeks) of *G. p. exilis*

Recruitment

Recruitment is the result of two processes: immigration and birth. Minimum recruitment per trapping occasion, calculated from MNA values, is presented in Fig. 6. Actual recruitment rates might be slightly lower since 46 % of the new captures were possibly transients (gerbils captured on fewer than 3 successive sampling occasions). However, since transients are arbitrarily defined, they are not analysed separately.

There was a marked increase in recruitment rate from October. The recruitment rate for the summer months (October 1981 to February 1982) was ≥ 0.20 per three weeks, leading to a considerable increase in population numbers. Recruitment was much lower during winter, averaging 0.09. The increased summer numbers can be attributed to adult immigration, the start of the breeding period and juvenile recruitment during the season. It

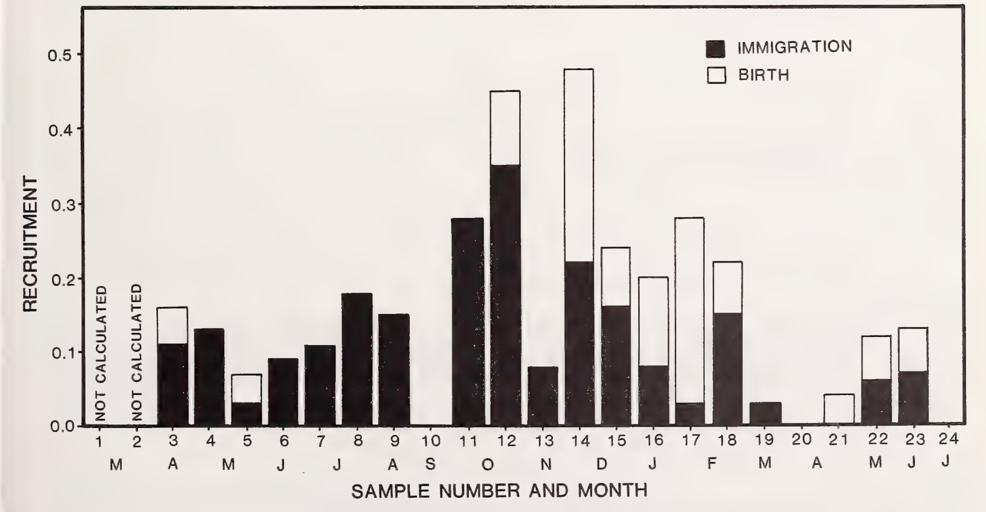


Fig. 6. Proportion of recruitment of *G. p. exilis* due to immigration and birth

is possible, to some extent, to distinguish birth and immigration, if newly-caught, young animals are regarded as juveniles and newly-caught adults are assumed to be immigrants. This division does not consider young immigrants or the fact that some individuals born in the area may not be captured until adulthood. Fig. 6 shows the likely proportions of recruitment due to immigration and birth. Juveniles first appeared at the end of October and formed a significant proportion of recruitment until the end of February. On average, however, immigration of older individuals appears to have played a greater role in recruitment than reproduction, the mean rates being 0.10 and 0.05, respectively. Christian (1980) reported one instance of large-scale immigration of *G. paeba* onto a trapping grid, but stated that generally, rates of growth in the populations he examined were sufficiently low to be explained in terms of breeding.

Population density

Population density has been measured as MNA per hectare. Because density can only be measured for the trappable population, the actual density of the gerbil population may be higher than the estimates given here. Allowance was made for individuals whose ranges lie on or near the borders of the sampling grid by the addition of a boundary strip. Average gerbil density was 1.7 gerbils/ha, with lowest density occurring in September (0.7/ha) and highest density in March (3.3/ha). Since only 50 % of the sampled area comprised suitable habitat, the densities were recalculated using an area of 7.25 ha, which represents the vegetated parts of the grid and boundary strip, where burrows occur. This gives an average density of 3.4 gerbils/ha (range: 1.4/ha–6.6/ha), or three gerbils per slack (range 1–7). Both density estimates approximate those of other rodents inhabiting sparsely vegetated areas. Minimum and maximum densities of the beach mouse, *Peromyscus polionotus leucocephalus*, were found to be 2.2/ha and 3.4/ha, respectively (Blair 1951). Chew and Chew (1970) in Delany (1976) give minimum and maximum densities of 0.4/ha and 3.3/ha for *Peromyscus eremicus*, a rodent inhabiting the Californian desert.

Conclusion

With 36 slacks in the Alexandria dunefield, the total population size of *G. p. exilis* is estimated at 108 (36–252) individuals, although this may be an underestimate. Since the Alexandria dunefield was declared a conservation area, the future of this small unique population seems favourable.

Acknowledgements

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Zusammenfassung

Populationsökologie des Rauhfußgerbills Gerbillurus paeba in einem Dünenfeld an der Küste von Südafrika

Untersucht wurde eine Population von Rauhfußgerbills, *Gerbillurus paeba*, von März 1981 bis Juli 1982 im Alexandria-Dünenfeld entlang der östlichen Kapküste von Südafrika. Hier ist *G. paeba* die einzig ständig vorkommende Nagetierart. Die Wiederfang-Studie einer markierten Population zeigte eine geringe Dichte von durchschnittlich 1,7 Gerbills/ha. Es findet ein jährlicher Populationswechsel statt. Die höchsten Fangzahlen wurden im Spätsommer, die geringsten im Spätwinter verzeichnet.

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Cytogenetics and karyosystematics of South American oryzomyine rodents (Cricetidae, Sigmodontinae)

III. Banding karyotypes of Argentinian *Oligoryzomys*

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Abstract

Studied the karyotypes of 86 specimens of *Oligoryzomys* cricetid mice from 15 different localities of Argentina. Four different chromosomal complements were found in the different samples. A polymorphic karyotype of 2n = 66–67–68 (FN = 68–69–70) assigned to *O. flavescens* showed large amounts of positive C-banding, two types of Y chromosomes and the presence of supernumerary elements in samples from the Buenos Aires province, Maimará (Jujuy) and El Infiernillo (Tucamán), enabling to assess the wide distribution and ecological versatility of this species. A karyotype of 2n = 58 (FN = 74) similar to a variant of *O. longicaudatus* described by Gardner and Patton from Perú, was found in samples from León (Jujuy) and from several lowland populations of Tucumán. They are provisionally considered to belong to *O. stolzmanni.* A karyotype of 2n = 56 (FN = 64, 66) similar to previously described karyotypes of *O. longicaudatus*, was found in samples from Tierra del Fuego and San Carlos de Bariloche. The cytotype variant of Tierra del Fuego proved to be identical to that of *O. longicaudatus philippi*, suggesting a lack of agreement between chromosomal differentiation and current subspecies recognition. A topotypical sample of *O. delticola* confirmed a karyotype of 2n = 62 (FN = 82) for this species.

Introduction

Rice rats currently assigned to the subgenus *Oligoryzomys* (genus *Oryzomys*) are widely distributed in Neotropica, and where they appear, they constitute an important component of its small mammal communities.

Notwithstanding its commonness and ecological importance, this taxon is certainly in an appalling state of confusion. Numbers of species comprised in *Oligoryzomys* vary, according to different authors, from just one (Hershkovitz 1966a; but see also Hershkovitz 1966b) to 31 (Tate 1932). Of the 31 species recognized by Tate, 12 are distributed from the south of Perú to Tierra del Fuego. Six of them are currently recognized in Argentina: *O. chacoensis, O. delticola, O. flavescens, O. fornesi, O. longicaudatus,* and *O. nigripes* (Honacki et al. 1982). Recently, partial revisions of related Paraguayan (Myers and Carleton 1981) and Bolivian (Olds and Anderson 1987) forms have contributed to clarification of their status. However, many problems still remain unsolved with regard to their taxonomy and nomenclature.

The aim of this paper is to contribute to a better knowledge of the Argentinian *Oligoryzomys* by the cytogenetic study of several samples belonging to four different species.

Material and methods

Cytogenetic analysis was performed on 86 mice of 15 different localities. They were collected with Sherman live traps and processed in the laboratory. Skin and skulls were deposited in the collection of

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mammals of the Museo Municipal de Ciencias Naturales "Lorenzo Scaglia" of Mar del Plata, Argentina. Species and localities given in Table 1.

Bone marrow chromosomal spreads were obtained following the current techniques, and stained with Giemsa. G- and C-bands were obtained following SEABRIGHT (1971) and SUMNER (1972), respectively. Chromosome lengths were expressed as percentage of the female haploid set (FHS), calculated from a minimum of 10 metaphases. Chromosome size classes followed REIG and KIBLISKY (1969): large (> 9 FHS), medium-sized (9–5.5 FHS), small 5.5–2 FHS), and microchromosomes (< 2 FHS). Chromosome nomenclature according to centromere position followed LEVAN et al. (1964). NF numbers are autosomal arm numbers.

Table 1. **Locality data for specimens of *Oligoryzomys* used in this study**

Species	Locality	Geographic coordinates	Chromosomically studied	
			Males	Females
O. flavescens	Paraná River Delta (Buenos Aires)	34° 10′ S; 71° 18′ W	7	4
	Monte Hermoso (Buenos Aires)	39° 02′ S; 61° 12′ W	5	2
	Capilla del Señor (Buenos Aires)	34° 16′ S; 59° 06′ W	2	1
	Diego Gaynor (Buenos Aires)	34° 18′ S; 59° 09′ W	5	1
	Río Cuarto (Córdoba)	33° 06′ S; 64° 22′ W	1	1
O. cf. *flavescens*	Maimará (Jujuy)	23° 35′ S; 65° 24′ W	1	4
	El Infiernillo (Tucumán)	26° 40′ S; 65° 46′ W	–	1
O. longicaudatus	S. C. de Bariloche (Rio Negro)	41° 11′ S; 71° 18′ W	2	–
	Bahía La Pataia (Tierra del Fuego)	54° 50′ S; 68° 26′ W	1	1
O. cf. *longicaudatus*	León (Jujuy)	24° 03′ S; 65° 26′ W	7	5
	Horco Molle y Quebrada de los Sosa (Tucumán)	26° 49′ S; 65° 15′ W	19	7
	El Cadillal (Tucumán)	26° 40′ S; 65° 16′ W	2	1
	Burruyacú (Tucumán)	26° 29′ S; 64° 45′ W	1	–
O. delticola	Delta del Río Parana (Buenos Aires)	34° 10′ S; 59° 14′ W	4	1

Results

Oligoryzomys flavescens. Most of the specimens analysed showed a karyotype of 2n = 66 (FN = 68) (Fig. 1) comprised of 32 pairs of autosomes and the XY sexual set. The first autosomal pair is a large (9.0 FHS) pair of chromosomes and clearly distinguishable from the second pair by a sharp size gap. The following series of 31 autosomal pairs are telocentric or acrocentric autosomes in which short arms are often difficult to distinguish, with the exception of two pairs of small and minute chromosomes in which a biarmed condition is evident in most cells (Table 2). This karyotype was the mode in 25 out of 29 studied specimens. Two males from Diego Gaynor, one female from Capilla del Señor,

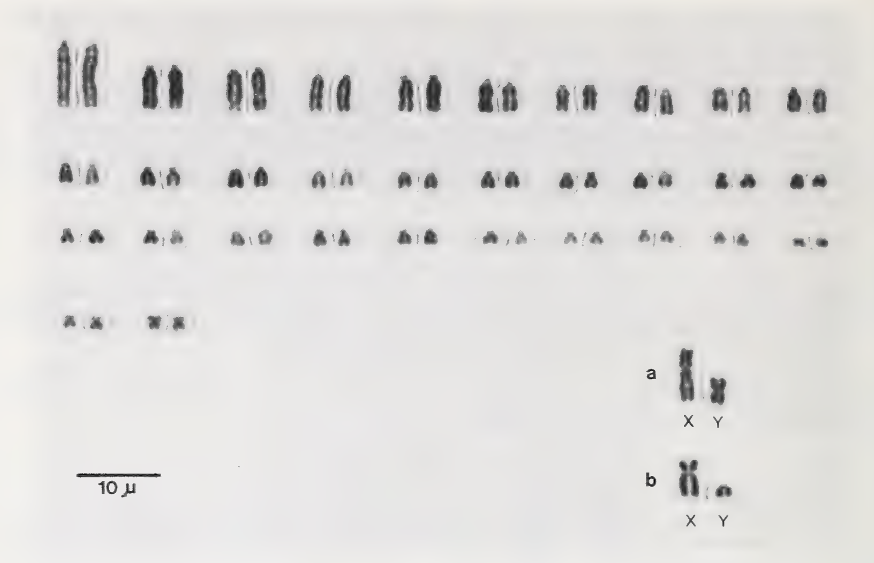


Fig. 1. Giemsa stained karyotype of *O. flavescens* from Diego Gaynor, Buenos Aires province. a and b: sexual set showing two types of Y-chromosome

and one female from Paraná River delta showed a 2n = 67 karyotype, with one small extra element (Fig. 2b). The sexual set was composed by a medium-sized submetacentric X (6.28 FHS) and two types of Y, telocentric and metacentric (Fig. 1) in both 2n = 66 and 67 karyomorphs. Each population was characterized by one of these Y-morphologies, except in Diego Gaynor and Paraná River delta samples, which proved to be polymorphic for the Y.

G- and C-banding are shown in Figure 2. C-banding showed that a sizable portion of the genome is C-positive. All autosomes showed pericentromeric C-bands and full C-positive short arms are also inferred in some of the autosomes. The extra element found in the 2n = 67 karyotype was fully C-positive, as well as the small arm and the pericentric region of the long arm of the X chromosome. While telocentric Y chromosomes were found to be C-positive, in the metacentric Ys only a terminal C-band in the small arm was found.

Oligoryzomys cf. *flavescens.* A karyotype similar to that described above, both in chromosomal number, gross morphology and banding patterns was found in female specimens from Maimará, Jujuy Province and from El Infiernillo, Tucumán Province. In the five specimens from Maimará diploid numbers ranged from 2n = 66 (FN = 68) to 2n = 68 (FN = 70), and the X was a medium-sized (6.4 FHS) submetacentric chromosome (Table 2). The single available female from El Infiernillo had a 2n = 68 (FN = 70) karyotype identical to the variant found in Maimará.

Oligoryzomys cf. *longicaudatus.* The specimens from León (Jujuy) and from Tucumanian localities other than El Infiernillo, showed an asymmetric 2n = 58 (FN = 74) karyotype (Fig. 3a). The autosomal set comprised 19 pairs of telocentric or acrocentric chromosomes and 9 pairs of biarmed elements. In the acrocentric series, the first pair was very close to the large class (8.8 FHS), bearing very small arms. It is clearly distinguishable by size from the following autosomes which gradually decrease in size from small to microchromosomes. Two elements of the biarmed series are large metacentrics, separated by an abrupt size gap from the seven following pairs, which are small to minute in size.

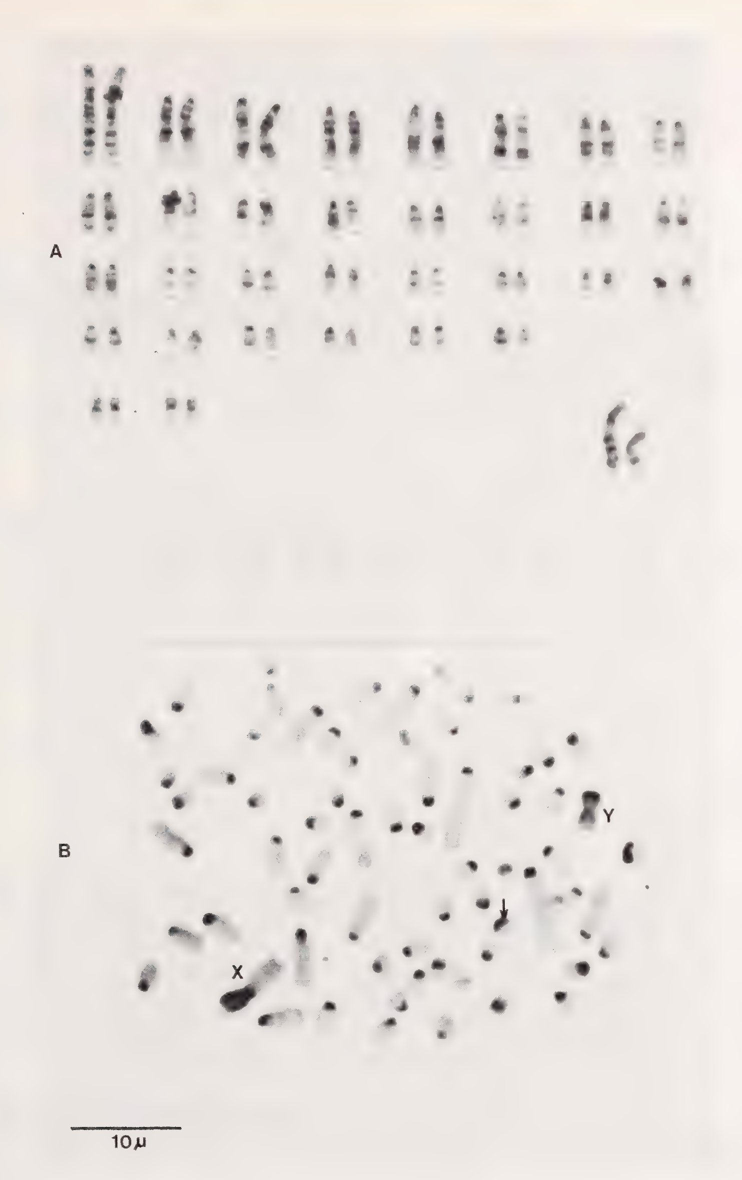


Fig. 2. A: G-banded karyotypes of *O. flavescens*. B: C-banded chromosomes of *O. flavescens* male 2n = 67 from Diego Gaynor, Buenos Aires province (arrow indicates the small extra element)

The X was a medium-sized submetacentric (7.6 FHS), and the Y a small-sized telocentric (2.6 FHS) (Table 3).

G-banding is shown in Figure 5. A preliminary arm-to-arm comparison showed that autosomes of the first acrocentric pair are homologous with the first pair of *O. flavescens*.

Oligoryzomys longicaudatus: A 2n = 56 (FN = 66) karyotype was found in specimens from Tierra del Fuego, with the autosomal set made of 21 telocentric or acrocentric pairs decreasing in size and 6 biarmed small-sized pairs (Figs. 3b, 6; Table 3). The first pair of acrocentrics corresponds very closely to the large class (8.8 FHS) and is separated from the

Table 2. **Chromosomal lengths of *Oligoryzomys flavescens* and *Oligoryzomys* cf. *flavescens* expressed as percentage of the female haploid set**

Chromosome	*O. flavescens* X ± SD	*O.* cf. *flavescens* X ± SD
1	9.0 ± 0.9	8.3 ± 0.6
2	6.1 ± 0.5	5.8 ± 0.3
3	5.6 ± 0.5	5.3 ± 0.2
4	5.0 ± 0.3	5.1 ± 0.2
5	4.7 ± 0.3	4.8 ± 0.1
6	4.3 ± 0.2	4.4 ± 0.2
7	3.8 ± 0.1	3.9 ± 0.1
8	3.5 ± 0.2	3.6 ± 0.2
9	3.4 ± 0.1	3.4 ± 0.2
10	3.2 ± 0.2	3.4 ± 0.2
11	2.9 ± 0.2	2.9 ± 0.1
12	2.7 ± 0.2	2.7 ± 0.2
13	2.5 ± 0.1	2.6 ± 0.2
14	2.5 ± 0.1	2.6 ± 0.2
15	2.4 ± 0.2	2.4 ± 0.1
16	2.3 ± 0.2	2.4 ± 0.1
17	2.3 ± 0.2	2.3 ± 0.1
18	2.1 ± 0.3	2.2 ± 0.1
19	2.0 ± 0.2	2.1 ± 0.2
20	2.0 ± 0.2	2.1 ± 0.2
21	1.9 ± 0.2	2.0 ± 0.2
22	1.9 ± 0.2	2.0 ± 0.2
23	1.8 ± 0.2	1.9 ± 0.1
24	1.7 ± 0.2	1.9 ± 0.1
25	1.7 ± 0.2	1.8 ± 0.1
26	1.6 ± 0.2	1.7 ± 0.2
27	1.5 ± 0.2	1.6 ± 0.1
28	1.5 ± 0.2	1.5 ± 0.1
29	1.4 ± 0.2	1.3 ± 0.1
30	1.3 ± 0.2	1.2 ± 0.2
31	2.2 ± 0.2 (1.4 ± 0.3)[a]	2.5 ± 0.3 (1.2 ± 0.1)
32	1.9 ± 0.3 (1.1 ± 0.2)	2.1 ± 0.3 (1.1 ± 0.2)
X	6.8 ± 0.6 (2.4 ± 0.4)	6.4 ± 0.9 (2.5 ± 0.9)
Y	3.8 ± 0.8 (1.4 ± 0.3)	3.5 ± 0.7 (1.5 ± 0.2)
Y[b]	2.6 ± 0.3	

[a] Number in parentheses indicates the centromeric index (long arm/small arm) of biarmed chromosomes. – [b] Telocentric Y.

following by a sharp size gap. The sexual set showed a medium-sized (6.5 FHS) subtelocentric X chromosome and a small (4.6 FHS) submetacentric Y. Specimens from Bariloche showed a similar 2n = 56 karyotype with fewer numbers of arms (FN = 64), and a submetacentric, instead of subtelocentric X chromosome. This suggests that both karyomorphs are interrelated by means of an autosomal pericentric inversion.

Oligoryzomys deltícola: Topotypes from the Paraná River delta showed a rather symmetrical 2n = 62 karyotype (FN = 82) made of 19 pairs of gradually decreasing small-sized and micro-acrocentric autosomes in which no short arms have been observed; and 11 biarmed autosomal pairs, ranging from medium sized to microchromosomes, including subtelocentric, submetacentric and metacentric autosomes (Fig. 4). The X was a medium-sized (6.2 FHS) metacentric chromosome and the Y a small (2.9 FHS) submetacentric chromosome (Table 3). G-banding is shown in Figure 7.

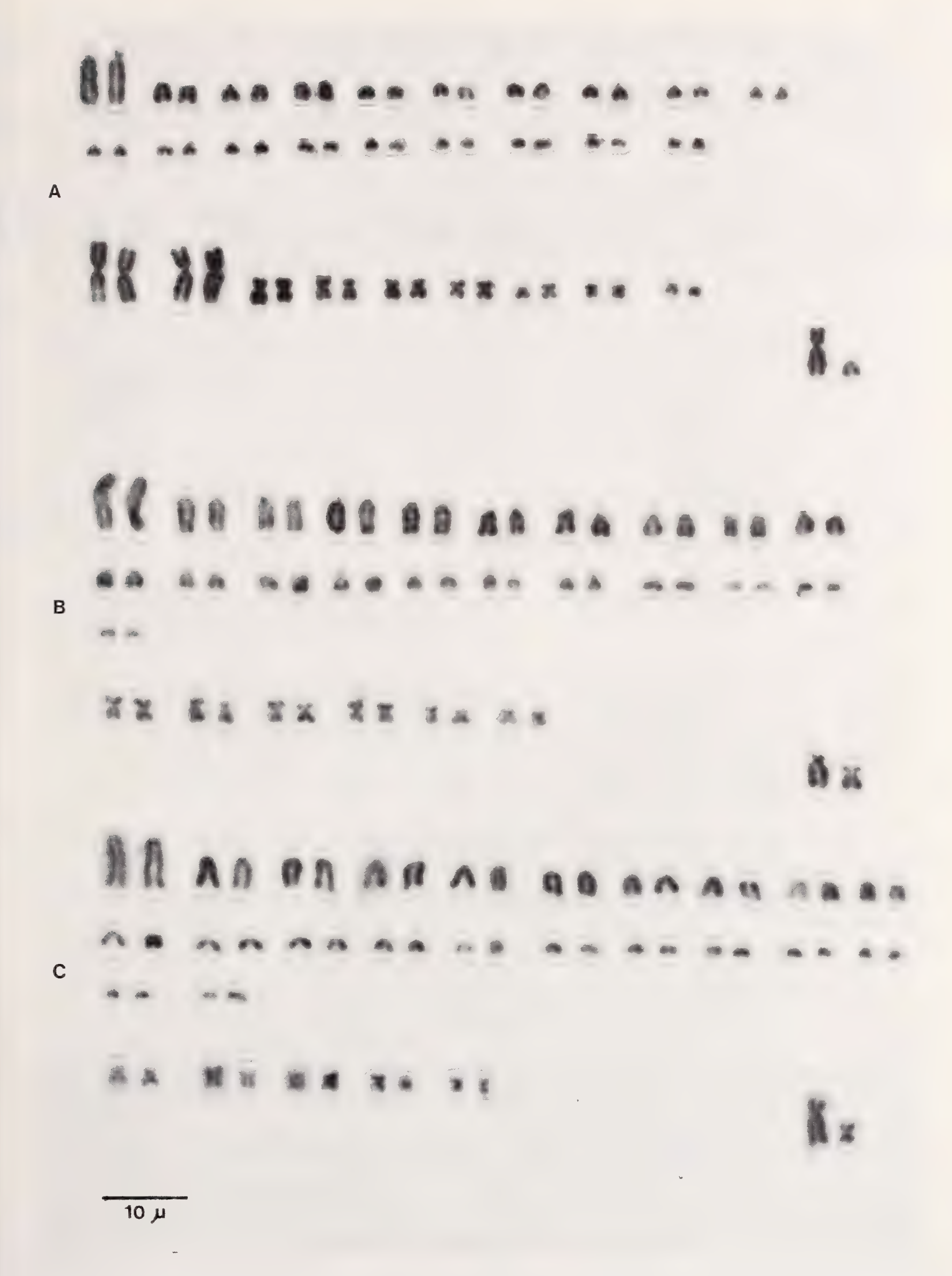


Fig. 3. Giemsa-stained karyotypes of: A: *Oligoryzomys* cf. *longicaudatus* from Horco Molle, Tucumán province (2n = 58, FN = 74). B: *O. longicaudatus* from Bahia La Pataia, Tierra del Fuego (2n = 56, FN = 66). C: *O. longicaudatus* from Bariloche, Rio Negro province (2n = 56, FN = 64)

Table 3. **Chromosomal lengths of *Oligoryzomys* cf. *longicaudatus, Oligoryzomys longicaudatus* and *Oligoryzomys delticola* expressed as percentage of the female haploid set**

Chromosome	*O.* cf. *longicaudatus* X ± SD	*O. longicaudatus* X ± SD	*O. delticola* X ± SD
1	8.8 ± 1.7	8.8 ± 0.3	4.9 ± 0.3
2	4.1 ± 0.2	5.9 ± 0.2	4.4 ± 0.2
3	3.6 ± 0.2	5.5 ± 0.3	3.8 ± 0.1
4	3.4 ± 0.2	5.3 ± 0.3	3.5 ± 0.2
5	3.1 ± 0.3	4.9 ± 0.2	3.2 ± 0.2
6	2.8 ± 0.2	4.3 ± 0.3	3.0 ± 0.1
7	2.6 ± 0.1	4.0 ± 0.2	2.8 ± 0.1
8	2.4 ± 0.2	3.8 ± 0.2	2.7 ± 0.1
9	2.2 ± 0.2	3.5 ± 0.2	2.6 ± 0.2
10	2.1 ± 0.1	3.3 ± 0.1	2.4 ± 0.1
11	2.0 ± 0.2	3.1 ± 0.1	2.4 ± 0.1
12	1.8 ± 0.1	2.8 ± 0.2	2.2 ± 0.1
13	1.8 ± 0.1	2.7 ± 0.1	2.1 ± 0.1
14	1.7 ± 0.1	2.5 ± 0.1	2.0 ± 0.1
15	1.7 ± 0.1	2.4 ± 0.1	2.0 ± 0.1
16	1.6 ± 0.1	2.2 ± 0.2	1.8 ± 0.1
17	1.6 ± 0.1	2.1 ± 0.2	1.7 ± 0.1
18	1.5 ± 0.2	2.0 ± 0.2	1.6 ± 0.2
19	1.3 ± 0.1	1.8 ± 0.1	1.3 ± 0.2
20	11.4 ± 0.8 (1.2 ± 0.1)[a]	1.6 ± 0.1	7.9 ± 0.4 (4.0 ± 0.5)
21	10.4 ± 0.8 (1.3 ± 0.1)	1.4 ± 0.1	6.2 ± 0.3 (5.0 ± 0.7)
22	4.5 ± 0.4 (1.1 ± 0.1)	4.1 ± 0.2 (1.2 ± 0.1)	6.0 ± 0.3 (2.0 ± 0.2)
23	3.6 ± 0.3 (1.4 ± 0.3)	3.8 ± 0.3 (1.2 ± 0.1)	3.9 ± 0.2 (1.8 ± 0.2)
24	3.4 ± 0.2 (1.3 ± 0.2)	3.6 ± 0.1 (1.3 ± 0.4)	3.7 ± 0.3 (1.4 ± 0.2)
25	3.1 ± 0.3 (1.1 ± 0.1)	3.2 ± 0.2 (1.1 ± 0.1)	3.5 ± 0.2 (1.1 ± 0.1)
26	2.5 ± 0.4 (1.2 ± 0.1)	2.8 ± 0.3 (1.3 ± 0.3)	3.3 ± 0.2 (1.2 ± 0.2)
27	2.0 ± 0.3 (1.2 ± 0.2)	2.4 ± 0.2 (1.3 ± 0.3)	3.0 ± 0.2 (1.1 ± 0.1)
28	1.7 ± 0.2 (1.0 ± 0.1)		2.3 ± 0.2 (1.3 ± 0.3)
29			2.1 ± 0.1 (1.1 ± 0.1)
30			1.7 ± 0.2 (1.0 ± 0.1)
X	7.6 ± 0.7 (2.4 ± 0.5)	6.5 ± 0.6 (3.3 ± 0.7)	6.2 ± 0.5 (1.3 ± 0.1)
Y	2.6 ± 0.4	4.6 ± 0.5 (1.4 ± 0.2)	2.9 ± 0.4 (2.3 ± 0.6)

[a] Numbers in parentheses indicate the centromeric index (long arm/small arm) of biarmed chromosomes.

Discussion

The karyotypes found in specimens of *O. flavescens* from different localities of Buenos Aires Province are quite similar to those described by Brum et al. (1977, 1988); Sbalqueiro et al. (1982, 1986) and Vidal Rioja et al. (1988) for populations of the same species from Uruguay and southern Brazil. The heteromorphism of the Y chromosome, as well as the presence of supernumerary elements found in those populations and in those studied by us, seem to be a feature of this species. A population study of a larger number of specimens would be necessary to determine the frequency of the two kinds of Y chromosomes, and the frequency and number of B chromosomes. Morphological variations of the sexual chromosomes do not seem to be unusual among oryzomyine rodents, as they have been observed in *O. nigripes, O. subflavus* and *O. longicaudatus* (Almeida et al. 1986; Svartman et al. 1986; Gallardo and Gonzalez 1977). Studies on sex chromosome variation particularly refer to the X chromosome (for a review, see Fredga 1988), and Y chromosome heteromorphism was reported in a few cases such as *Clethrionomys* (Arvicolidae) (Vorontzow and Lyapunova 1978) and *Proechimys* (Caviomorpha) (Reig

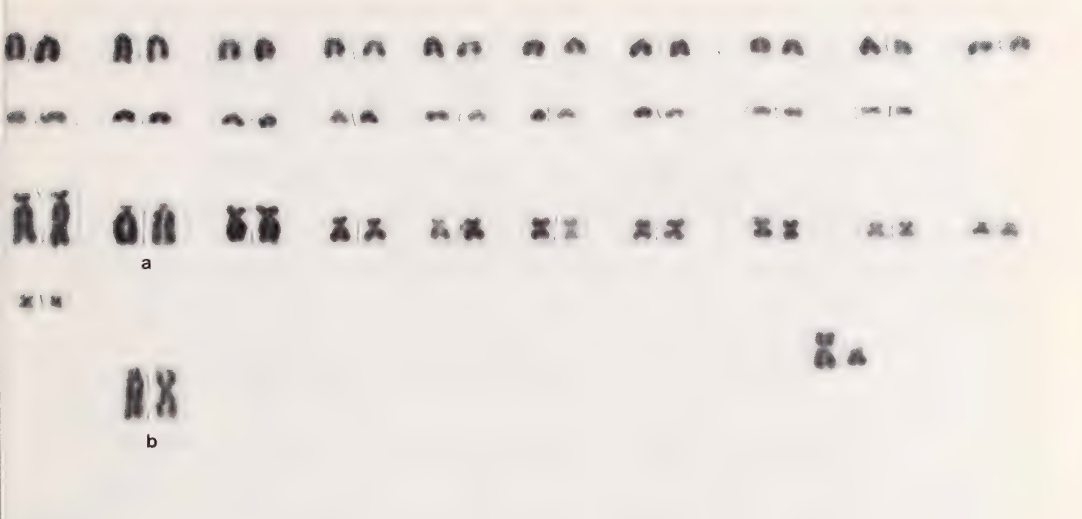


Fig. 4. Giemsa-stained karyotype of O. *delticola* from Paraná Delta River (2n = 62, FN = 82). a and b: pair 21 heteromorphic with pericentric inversion

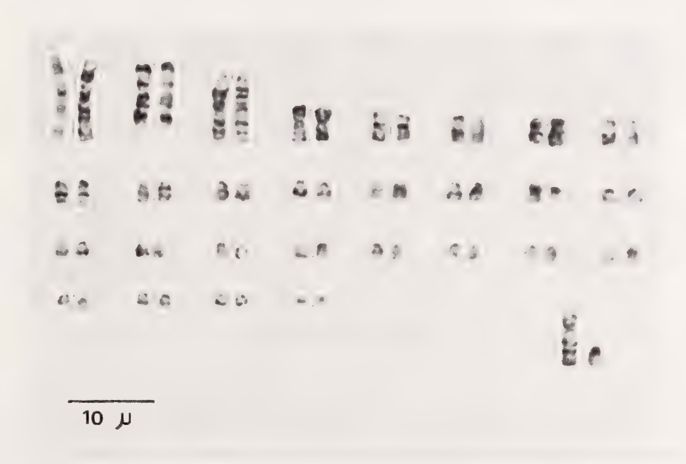


Fig. 5. G-banded karyotype of O. cf. *longicaudatus* from León, Jujuy province

et al. 1980). B chromosomes are of rare occurrence in mammals (Jones and Rees 1982). In rodents, they have been reported in *Perognathus* (Patton 1977), *Apodemus peninsulae* (Bekasova et al. 1978), *Akodon mollis* (Lobato et al. 1982), *Nectomys squamipes* (Maia et al. 1984) and a few other examples. The observations of Sbalqueiro et al. (1986) indicate that the supernumerary elements vary among different populations of O. *flavescens.*

The karyotypes found in the Maimará and El Infiernillo samples are quite similar to those reported for O. *flavescens* and corroborated by us in different populations of the province of Buenos Aires. This similarity allows to assert that there is no cytologic barriers between these populations.

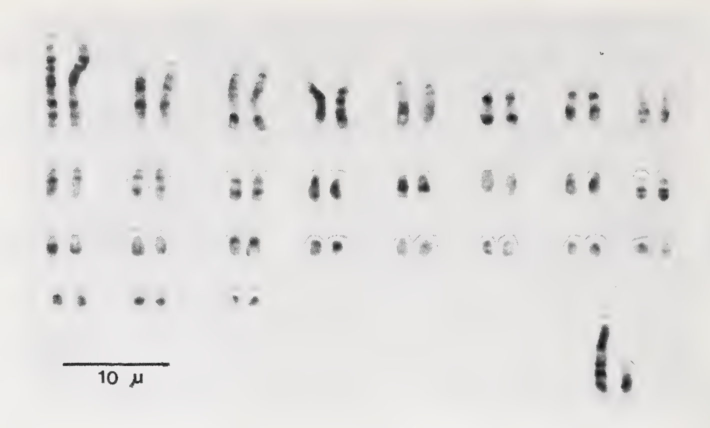


Fig. 6. G-banded karyotype of *O. longicaudatus* from Bariloche, Rio Negro province

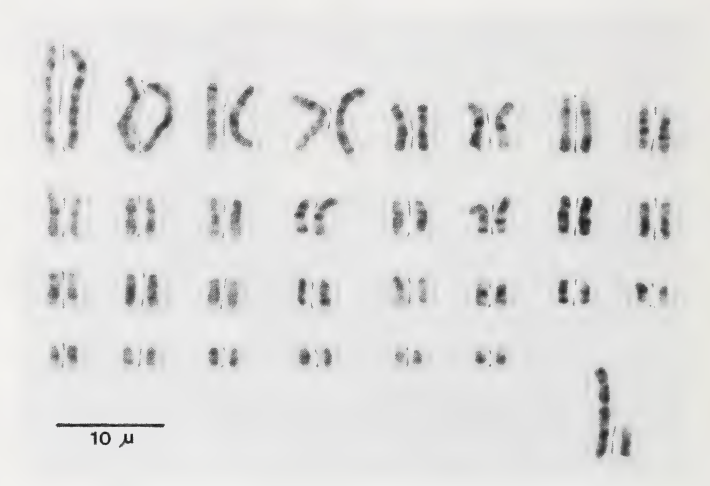


Fig. 7. G-banded karyotype of *O. delticola* from Paraná River delta, Buenos Aires province

Myers and Carleton (1981) found a great morphological similarity between *O. flavescens* and *O. fornesi*, and they questioned the species distinction of the latter. However, they found some karyological differences between them based on the karyotype of *O. flavescens* previously described by Brum (1965). However, this karyotype was based on old and unreliable techniques. In fact, the karyotype described by these authors for *O. fornesi* from Paraguay is basically the same, that we found for *O. flavescens* and *O.* cf. *flavescens* from Argentina, and it also fully agrees with the karyotype of *O. flavescens* from Uruguay recently described by Brum et al. (1988). Thus, our results support the doubt of Myers and Carleton (1981) on the validity of *O. fornesi*. The issue is further complicated by the claim of Olds and Anderson (1987) that *O. fornesi* is a synonym for *O. microtis*, which they consider a different species from *O. flavescens*, so that at the present state of our knowledge it is wiser to think of *O. fornesi* at least as a subspecies of *O. flavescens*.

The karyotype found for *O. longicaudatus*, of Tierra del Fuego, which should be referred to as the subspecies *O. l. magellanicus*, is identical to that described by Gallardo and González (1977) for the subspecies *O. l. philippi* from Valdivia, Chile. It is also

intriguing that OLIVERO (1985) found a karyotype of *O. longicaudatus* from Isla Redonda, Tierra del Fuego (which should be identified as *O. l. magellanicus*, see OSGOOD 1943), which matches the variant that we found in Bariloche (which should be classified as *O. l. longicaudatus*). Thus, the chromosomal data seems to indicate that there is no correspondence between subspecies recognition and karyotypic differentiation in *O. longicaudatus*.

Notwithstanding its gross general resemblance, the karyotype of 2n = 58 (FN = 74) found in populations of León (Jujuy province) and Tucumán (other than El Infiernillo) differs significantly from the typical representatives of this species from Chile and Tierra del Fuego (GALLARDO and PATTERSON 1985). These differences are large enough to suggest that we are dealing with a different species. The karyotype more closely related to that of León and the lowland Tucumanian localities is the variant (4) karyotype of *O. longicaudatus* described by GARDNER and PATTON (1976) in specimens from Huanhuacchayo, Dto. Ayacucho, Perú at an altitude of 1,660 m above sealevel. The León and Tucumanian karyotype only differs from the Peruvian one by possessing one pair of telocentric elements. Therefore, it is likely that the Peruvian, Leonian and Tucumanian cytotypes belong to the same species. As regards the name to apply to this species, a definite solution is probably untimely in view of the dubious situation of nominal forms such as *O. stolzmanni*, *O. destructor* and *O. microtis* (see OLDS and ANDERSON 1987). A conventional solution would be to refer to these cytotypes as *O. stolzmanni*, found in Huambo, Dept. of Amazonas, Perú at 1,133 m. The specimens from León are within the same height range and belong to similar habitats.

The karyotypes found in *O. delticola* from the type locality matches perfectly those described in previous reports for South Brazil (SBALQUEIRO et al. 1982, 1986) and Uruguay (BRUM et al. 1988). We also confirmed this karyotype in one female circumstantially caught in Salto, Uruguay, which showed a heteromorphic variant at pair 21 with one of the autosomes affected by a pericentric inversion. No heteromorphism in the topotypical specimens was found, but in view of the small size of the studied sample, we cannot discard its occurrence in that locality.

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Zusammenfassung

Zytogenetik und Karyosystematik von südamerikanischen Reisratten (Cricetidae, Sigmodontinae). III. Banden-Karyotypen von argentinischen Oligoryzomys

Untersucht wurden die Karyotypen von 86 Exemplaren der Cricetiden-Gattung *Oligoryzomys* aus 15 Fundorten in Argentinien. Vier verschiedene chromosomale Typen wurden gefunden. Ein polymorpher Karyotyp mit 2n = 66–67–68 (FN = 68–69–70), der *O. flavescens* zugeschrieben wurde, zeigte eine große Anzahl von C-Banden, zwei Typen von Y-Chromosomen und Auftreten zusätzlicher Elemente in den Stichproben aus der Provinz Buenos Aires, aus Maimará (Jujuy) und aus El Infiernillo (Tucumán). Durch diese Befunde konnte die weite Verbreitung und die ökologische Vielseitigkeit dieser Art bestätigt werden. Im Sammlungsmaterial von León (Jujuy) und bei mehreren Tieflandpopulationen aus Tucumán ergab sich ein Karyotyp mit 2n = 58 (FN = 74), der einer Varianten von *O. longicaudatus* ähnelt, die GARDNER und PATTON in Peru fanden. Er wurde vorläufig *O. stolzmanni* zugeordnet. Für die Individuen von Feuerland und San Carlos de Bariloche wurde ein Karyotyp mit 2n = 56 (FN = 64–66) ermittelt, der dem früher beschriebenen von *O. longicaudatus* gleicht. Die Variante des Karyotyps von Feuerland scheint identisch mit der von *O. longicaudatus philippi*. Dieses legt den Schluß nahe, daß zwischen chromosomalen Differenzierungen und der aktuellen Kennzeichnung von Unterarten keine Übereinstimmung besteht. Ein topotypischer Fund von *O. delticola* bestätigte für diese Art einen Karyotyp mit 2n = 62 (FN = 82).

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WISSENSCHAFTLICHE KURZMITTEILUNG

Sex ratio in newborn Common marmosets *(Callithrix jacchus)*: no indication for a functional germ cell chimerism

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The compilation of marmoset and tamarin breeding data from several different sources shows a deviation from the expected 1:1 sex ratio in favour of males (e.g. Ford and Evans 1977; citation of unpublished data from different colonies; Gengozian 1971; Gengozian et al. 1980; Hampton 1970; for additional references and discussion see Rothe et al. 1991).

The question was asked whether a skewing of the sex ratio in marmosets and tamarins could be due to germ cell chimerism, i.e. in the case of an excess of males due to XY oocytes, in the case of an excess of females due to XX spermatocytes (detailed discussion see Ford and Evans 1977; Gengozian 1971; Gengozian et al. 1980; Hampton 1970; Hampton 1973). Different opinions exist, however, whether germ cell chimerism in callitrichids is functional or not (detailed discussion in Gengozian et al. 1980). According to Gengozian et al. (1980) germ cell chimerism in callitrichids is a very rare event. Furthermore, these authors observed a balanced sex ratio in known heterosexual chimeras, and they could not identify unequivocally XX or XY cells at diakinesis-metaphase in the primary spermatocytes or oocytes, respectively, of *Saguinus oedipus* and *Saguinus fuscicollis* chimeras. These results provide presumptive evidence against functional germ cell chimerism (at least) in these species.

One major problem in analysing the reasons of a skewed sex ratio are not only lacking data on the frequency of known chimeras in the respective breeding colony, but often also an insufficient number of offspring born to each breeding pair and of the entire colony.

The composition and size of 114 litters (= 297 infants) were analysed. Litters of unknown size and/or sex ratio were excluded from the investigation. The breeding males (n = 30) and the breeding females (n = 30) were all born in captivity (filial generation F_1 to F_6) and were grouped into two categories: a. males/females that were born in isosexual litters and b. males/females that were born in heterosexual litters. Accordingly, the breeding pairs were grouped into four categories: A. both parents were born in isosexual litters; B. the father was born in an isosexual, the mother in a heterosexual litter; C. the father was born in a heterosexual, the mother in an isosexual litter; D. both parents were born in heterosexual litters (see Table).

Housing and feeding of our marmoset colony have already been described elsewhere in detail (Rothe et al. 1991).

Chi²-test was used to test differences between expected and observed frequencies of newborn males and females (Siegel and Castellan 1988).

The table shows the number of litters and infants according to litter-size, litter-composition and origin of the parents (categories A to D). Except for category C (χ^2 = 5.76; df = 1; $P < 0.05$) there were no significant differences in the sex ratio of newborn

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marmosets (see also ROTHE et al. 1991) and further, no indication of a secondary sex-ratio manipulation due to germ cell chimerism in either the males or the females was found, i.e. groups with a parent that was born in a heterosexual litter did not show a shift in the sex ratio to either males (category B) or females (category C).

Thus, our data do not provide a basis for the assumption that one or the other breeding male deviated from the 1:1 ratio of X- or Y-containing sperm cells, or that one or the other female produced Y-containing ova. The data suggest that germ cell chimerism in the common marmoset is a rare event which generally seems to have no impact on the overall sex-ratio of the population. However, due to the rather small sample size, expecially concerning the number of litters of each female, we cannot exclude that germ cell chimerism occurs in some males and females and hence might be of some importance for the sex ratio of their offspring. This aspect needs further investigation.

Number of litters and infants according to litter-size, litter-composition and origin of the parents

	Litter-size and -composition	Categories A	B	C	D	Σ litters	Σ infants
Singletons	m	0	1	0	2	3	3
	f	0	0	0	4	4	4
Twins	mm	2	1	2	3	8	16
	mf	6	4	4	8	22	44
	ff	1	3	2	1	7	14
Triplets	mmm	1	0	5	5	11	33
	mmf	5	3	4	14	26	78
	mff	3	1	7	13	24	72
	fff	0	0	0	3	3	9
Quadruplets	mmmm	0	0	0	1	1	4
	mmmf	0	0	0	0	0	0
	mmff	0	0	1	1	2	8
	mfff	0	0	0	2	2	8
	ffff	0	0	0	1	1	4
	Σ litters	18	13	25	58	114	—
	Σ infants	45	29	68	155	—	297
	sex-ratio (m:f)	1.34:1.0	0.93:1.0	1.43:1.0	1.07:1.0	—	1.17:1.0

m = male; f = female; m:f = ratio of males to females; category A: both parents were born in isosexual litters; category B: father was born in an isosexual litter, mother in a heterosexual; category C: father was born in a heterosexual litter, mother in an isosexual; category D: both parents were born in heterosexual litters.

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Symbiogenese als Motor der Evolution

Grundriß einer Theoretischen Biologie

Von Prof. Dr. Werner Schwemmler, Institut für Pflanzenphysiologie, Zellbiologie und Mikrobiologie, Freie Universität Berlin

Biologie und Evolution interdisziplinär

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Das Buch beschreibt die Evolution – vom Urknall über Teilchen, Atome, Moleküle und Zellen bis hin zum Menschen – teils als fließenden oder graduellen, teils als sprunghaften bzw. punktuellen Prozeß. Evolution ist das Ergebnis nicht nur bekannter Mikromechanismen (Gradualismus), sondern auch übergeordneter Meso- und Makromechanismen (Punktualismus). Das Modell einer vereinheitlichten Theorie der Evolution, das sich an die großen vereinheitlichten Theorien der Natur von den Physikern anschließt, wird auf der Grundlage dieser Typen von Mechanismen abgeleitet.
Dieses Modell kann als Basis für eine moderne Theoretische Biologie dienen, deren Kernstück intrazelluläre Symbiosebildungen sind, d.h. Vergesellschaftungen zellulärer Systeme, die Endocytobiosen. Die Strukturen und Funktionen von Endocytobiosen folgen Mustern, die ihre Einordnung in ein Periodensystem der Zellen erlauben.
Aus der Endocytobiologischen Zelltheorie ergeben sich neue experimentelle Ansätze zum Studium von Eientwicklung, Krebsbildung und innerer Zelluhr. Die moderne Forschungsrichtung Endocytobiologie leistet einen Beitrag zur fächerübergreifenden Analyse dieser noch ungelösten Rätsel der Biologie.

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ZEITSCHRIFT FÜR SÄUGETIERKUNDE

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Zusätzlich erscheint einmal im Jahr ein Heft mit den Abstracts der Vorträge, die auf der jeweiligen Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde gehalten werden. Sie werden als Supplement dem betreffenden Jahrgang der Zeitschrift zugeordnet. Verantwortlich für ihren Inhalt sind ausschließlich die Autoren der Abstracts.

Manuskripte: Manuskriptsendungen sind zu richten an die Schriftleitung, z. Hd. Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Biologie-Zentrum, Neue Universität, Olshausenstr. 40–60, W-2300 Kiel, Bundesrepublik Deutschland. Für die Publikation vorgesehene Manuskripte sollen gemäß den „Redaktionellen Richtlinien“ abgefaßt werden. In ihnen finden sich weitere Hinweise zur Annahme von Manuskripten, Bedingungen für die Veröffentlichung und die Drucklegung, ferner Richtlinien für die Abfassung eines Abstracts und eine Korrekturzeichentabelle. Die Richtlinien sind auf Anfrage bei der Schriftleitung und dem Verlag erhältlich.

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The origin of the Australian Vespertilioninae bats, as indicated by chromosomal studies

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Abstract

Two species of Australian vespertilionids were karyologically studied, *Falsistrellus tasmaniensis* and *Scotorepens balstoni*. The *Falsistrellus* karyotype is composed of 44 chromosomes and, apart from some minor differences, is identical with those of other Australian Vespertilioninae described previously. *Scotorepens balstoni* displays a unique karyotype consisting of 30 chromosomes.

All Australian Vespertilioninae examined so far share an altered chromosome 11, which when compared with several vespertilionid genera has been shown to represent the derived state and to be a synapomorphic feature of the tribe Vespertilionini. Therefore, the genera *Nyctophilus, Chalinolobus, Falsistrellus, Scotorepens* and the *Pipistrellus* subgenus *Vespadelus*, which are restricted to Australia and New Guinea, belong to the Vespertilionini tribe. Because true members of the genus *Pipistrellus* do not belong to this tribe, the elevation of the subgenus *Vespadelus* to the generic level is proposed. The close phylogenetic relationships of the morphologically rather distinct genera, together with their limited distribution, point to a common origin of all Australian Vespertilioninae, followed by adaptive radiation.

Introduction

During the last decade, several studies dealing with morphometric or electrophoretic data of Australian vespertilionids have been published. These studies have resulted in e.g. descriptions of new species or changes in generic status, raising the number of Australian vespertilionid species to 34, belonging to 11 genera. These changes in systematic position of Australian genera are briefly summarized below.

For a long time, because of their dental formula, the smallest Australian "pipistrelloid" species have been placed in the genus *Eptesicus*. The number of recognized species in this group was considerably enlarged by a morphological approach, supported by electrophoretic studies (Kitchener et al. 1987; Adams et al. 1987). Due to the shape of the bacula, Hill and Harrison (1987) transferred the Australian "*Eptesicus*" to a separate subgenus of *Pipistrellus*, i.e. *Vespadelus*. In a previous study we supported this view (Volleth and Tidemann 1989). However, additional chromosomal data obtained in the meantime (Volleth 1989) and the results of the present paper support the elevation of *Vespadelus* to the generic rank.

The large-sized *Pipistrellus tasmaniensis*, now considered to consist of two distinct species *(tasmaniensis, mackenziei)*, has been shown to be phenetically and phylogenetically quite distinct from the Australian members of "*Pipistrellus tenuis*", which themselves have been split into two species restricted to Australia (*P. westralis, P. adamsi*; Kitchener et al. 1986). Therefore, Kitchener et al. (1986) resurrected *Falsistrellus* Troughton, 1943 as the generic name for *tasmaniensis* and *mackenziei*.

Because of morphological similarities *Nyctophilus* was once thought to be closely allied to the New World genus *Antrozous*; both were regarded as members of the subfamily Nyctophilinae (Miller 1970; Tate 1942). Koopman (1984), however, removed *Antro-*

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zous and changed the status of the subfamily into a tribe, Nyctophilini, placed within the Vespertilioninae.

The Australian members of the Nycticeiini have formerly been placed with *Scotophilus* and *Scoteinus* (for references see Kitchener and Caputi 1985). Since the study of Laurie and Hill (1954), they have been referred to the genus *Nycticeius*, which also includes species living in Africa and North America. After morphometric studies, involving several members of the tribe, Kitchener and Caputi (1985) placed the Australian species into two distinct endemic genera, *Scotorepens* and *Scoteanax*, erected by Troughton (1943).

This paper deals with chromosomal data of two endemic species, *Falsistrellus tasmaniensis* (Gould, 1858) and *Scotorepens balstoni* (Thomas 1906). The results, together with those of a previously published study (Volleth and Tidemann 1989), enable us to suppose that three quarters of the Australian vespertilionid species have evolved from a common ancestor. This adaptive radiation is comparable, although with considerably fewer species involved, with the radiation of the Corvi (Passeres, Aves) during the Tertiary in Australia (Sibley and Ahlquist 1985).

Materials and methods

The animals were collected from free-living populations in 1989. The specimens are deposited in the Senckenberg-Museum, Frankfurt/Main (SMF) (accession numbers in parentheses).

Specimens examined: *Falsistrellus tasmaniensis* (Gould, 1858), Bull's Head, Australian Capital Territory, 34° 24′ S, 148° 50′ E (male, SMF 77897); *Scotorepens balstoni* (Thomas 1906), Double Tanks, Willandra Lakes Region, New South Wales, 33° 42′ S, 142° 54′ E (two males, SMF 77898 and 77899).

Metaphases were obtained from fibroblast cultures of heart and lung biopsies. Culture conditions as well as chromosome preparation and staining procedures are described elsewhere (see Volleth and Tidemann 1989). For the calculation of the FN (fundamental number) completely heterochromatic arms have not been taken into account. The chromosome arms were numbered according to Bickham (1979a). Comparison of the G-banding pattern of *Myotis* with those of other vespertilionid genera revealed clear differences in eight chromosomes caused by peri- or paracentric inversions. The chromosome present in *Myotis* was called "state I" and the homologous chromosome in another genus, if altered by an inversion, was called "state II" of the chromosome in question. These differences (state I vs. state II) were used as characters for an evaluation of the intergeneric relationships of the Vespertilionidae (Volleth 1989).

Results

Falsistrellus tasmaniensis (2n = 44, FN = 52)

This species possesses a karyotype with 44 chromosomes, composed of three large and one small metacentric and 17 acrocentric autosomal pairs. A G-banded karyotype is shown in Fig. 1.

Compared to the G-banding pattern of *Myotis* (Bickham 1979a), differences were found on chromosomes 1/2, 11, 12, 15 and the X, here all present in state II, as is the case with other Australian species, e.g. *Chalinolobus morio* (see Volleth and Tidemann 1989). Chromosome 7, however, shows an euchromatic short arm, clearly visible in CBG-banded metaphases (Fig. 2a), as in *Myotis* and *Vespadelus vulturnus* and *darlingtoni* (Volleth and Tidemann 1989, the species *sagittula* studied in that paper was synonymized with *darlingtoni* by Kitchener et al. 1987). Some of the CBG-banded metaphases showed a weak interstitial heterochromatic band in the proximal region of chromosome 6 (Fig. 2a). One of the two smallest chromosome pairs (i.e. 24, 25) has acquired a large amount of heterochromatic material. One arm of the resulting biarmed chromosome is completely heterochromatic and of the size of arm 18; the second arm consists of euchromatic material in the proximal part (presumably the material of arm 25) and of C-

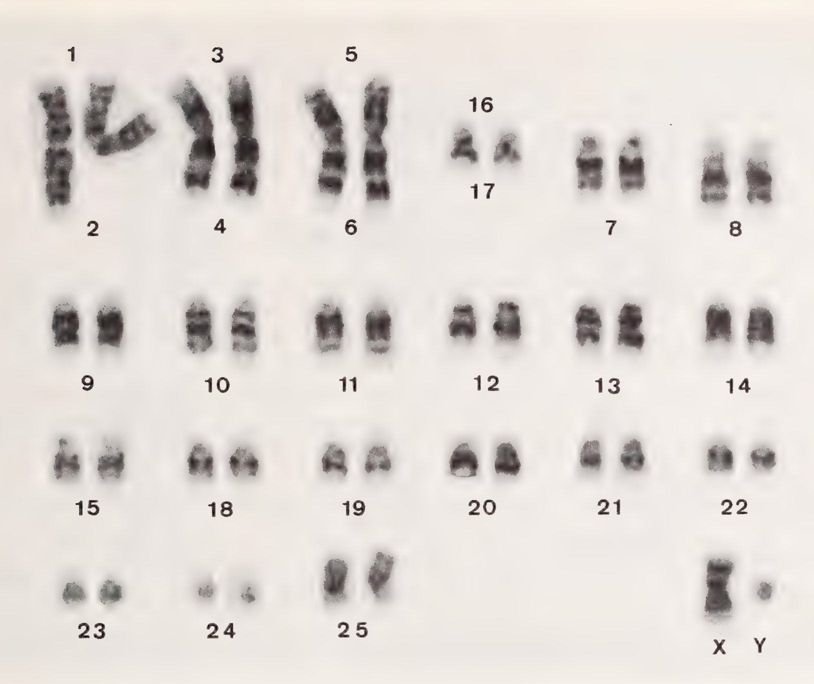


Fig. 1. G-banded karyotype of a male *Falsistrellus tasmaniensis*

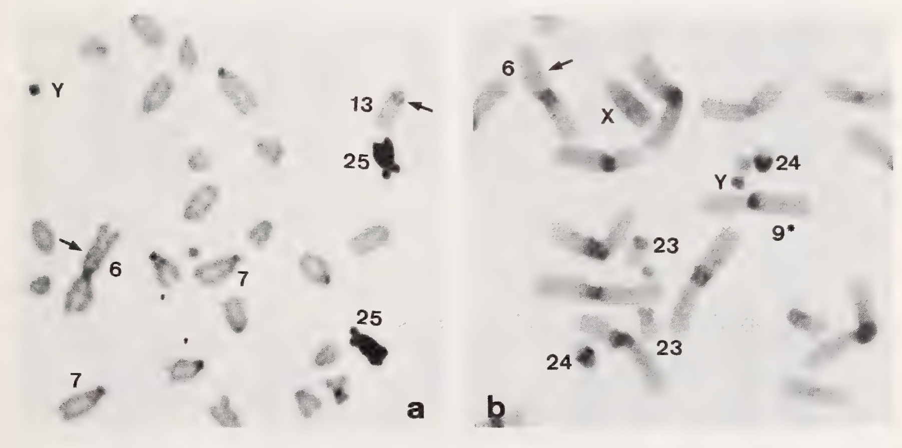


Fig. 2. Partially C-banded metaphases of *Falsistrellus tasmaniensis* (a) and *Scotorepens balstoni* (b). a: The arrows indicate faint interstitial heterochromatic bands on arm 6 and 13. Please note the tiny euchromatic short arm on chromosome 7 and the large heterochromatic blocks on chromosomes 25; b: The enlarged regions of centromeric heterochromatin on several chromosomes are clearly visible. The arrow points to the small interstitial heterochromatic band on arm 6

positive material in the distal part (Fig. 2a). The Y-chromosome is metacentric, of the same size as chromosome 24 and largely heterochromatic (Fig. 2a).

A slight difference from other vespertilionid karyotypes was found on chromosome 13. This chromosome shows two GTG-positive blocks, one proximal and one distal. In the

case of *Falsistrellus tasmaniensis* the proximal block is not, as is usually the case, divided into two subbands, but into three. The most proximal subband is very clearly separated from the others by a GTG- and QFQ-negative, and CBG-positive interband. This might be the result either of heterochromatic addition to the originally proximal situated subband or of a small paracentric inversion followed by addition of heterochromatic material.

The Nucleolus Organizer Region (NOR) is situated in the secondary constriction of chromosome 15.

Scotorepens balstoni (2n = 30, FN = 48)

The karyotype consists of 30 chromosomes and is composed of six large meta- to submetacentric, four medium to small submetacentric and four small acrocentric autosomal pairs. The arrangement of autosomal arms involved in biarmed chromosomes was traced to be 1/2, 7/4, 12/6, 13/8, 9/5, 14/11, 15/10, 21/3, and 22/20. Of the acrocentric chromosomes, arms 23, 24 and 25 were identified. The composition of two chromosomes, one submetacentric (called "A" in Fig. 3) and one acrocentric ("B"), remained unclear. Those arms, which were found to exist in two states in the Vespertilionidae, are present here in state II (1/2, 7, 11, 12, 15).

The X-chromosome is a large acrocentric and the Y-chromosome is a small metacentric chromosome. A G-banded karyotype is shown in Fig. 3.

In addition to two Robertsonian fissions and eight centric fusions, responsible for the reduction of the diploid chromosome number, one paracentric inversion (arm 1), one centromere shift (X-chromosome) and heterochromatic addition on several chromosomes occurred during the chromosomal evolution of this species. The inverted segment on

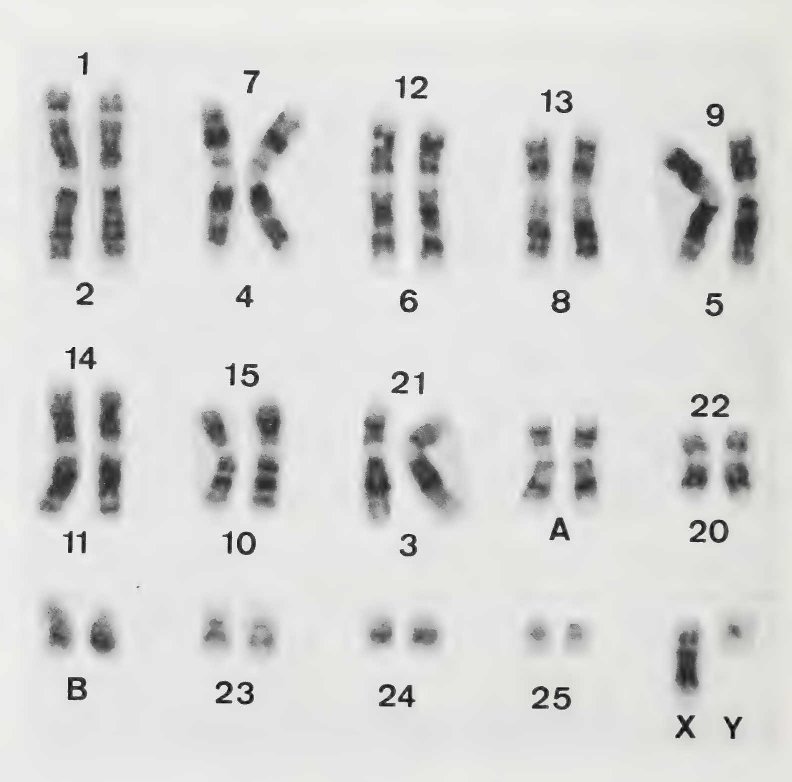


Fig. 3. G-banded karyotype of a male *Scotorepens balstoni*

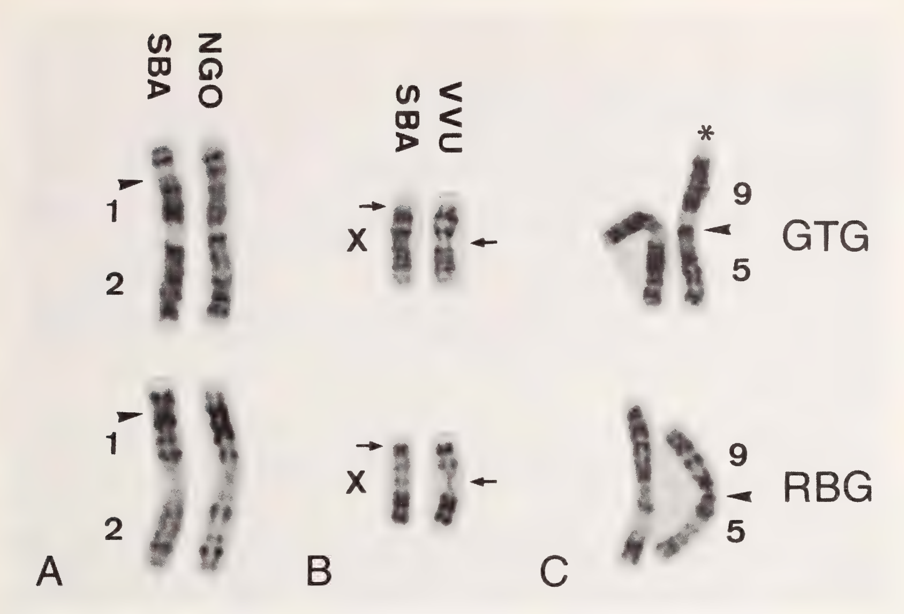


Fig. 4. Peculiar *Scotorepens balstoni* (SBA) chromosomes. Upper row: GTG-banding; lower row: replication banding (RBG). A: Chromosome 1/2 of SBA (left) compared with that of *Nyctophilus gouldi* (NGO, right). The arrow points to the proximal end of the inverted portion. B: X-chromosome compared with the X of *Vespadelus vulturnus* (VVU). The arrows indicate the position of the centromeres. C: Polymorphism on chromosome pair 9/5 in SBA. The right chromosome (indicated by a star) shows an additional segment on arm 5, close to the centromere, indicated by the arrowhead. Further explanations see text

chromosome 1/2 is located in the terminal region of arm 1, as can be clearly seen when compared with the unaltered homologous chromosome of *Nyctophilus gouldi* (Fig. 4A). The centromere shift or centromere transposition, which moved the centromere to the formerly telomere region of the short arm of the X-chromosome, can be demonstrated when the metacentric X of *Vespadelus vulturnus* is compared with it (Fig. 4B). In this case, only replication banding (RBG) is appropriate to show that the altered chromosome cannot be derived by a simple inversion. A polymorphic feature was detected on chromosome pair 9/5. Both specimens examined showed one "normal" chromosome and one with an additional segment in the proximal region of arm 5. This small segment was characterized as GTG-, RBG- and CBG-positive and CMA-negative (Fig. 4C). The origin of this segment remains unclear.

In 11 out of the total of 14 autosomal pairs the amount of centromeric heterochromatin is increased. These regions are completely GTG-negative and late replicating. They are CBG-positive and showed bright fluorescence after staining with chromomycin A. Only chromosomes 15/10, 22/20 and 25 lack these regions. As in *Falsistrellus*, a faint interstitial C-positive band was detected on arm 6 (Fig. 2b). The proximal half of the small acrocentric chromosome 24 is CBG-positive. The small Y-chromosome appears to be totally heterochromatic (Fig. 2b).

The NOR-bearing secondary constriction is situated in the long arm of chromosome 23 close to the centromere, resulting in a clear enlargement of this chromosome when compared to that of other Australian vespertilionids.

Discussion

A comparison of the karyotypes of the Australian vespertilionid genera examined so far revealed extensive complete arm homologies (see also VOLLETH and TIDEMANN 1989). With the exception of a few minor differences, the chromosomal complement is identical in *Chalinolobus, Nyctophilus, Falsistrellus* and *Vespadelus*. Small amounts of additional heterochromatic material observed in *Chalinolobus morio* and in *Falsistrellus tasmaniensis* are located on different chromosomal pairs. A common feature present in *Falsistrellus* and *Vespadelus* is the euchromatic short arm on chromosome 7, which can be derived from the chromosome present in the other Australian genera by means of a pericentric inversion.

In contrast, several chromosomal rearrangements were found in the karyotype of *Scotorepens balstoni*, leading to a diploid chromosome number of 30. Most of the chromosomal arms, however, were found to be identical with those of the above mentioned genera.

A comparative cytogenetic study of about 20 vespertilionid genera (VOLLETH 1989) revealed a small but sufficient number of features suited for karyological characterization of tribes and subfamilies. According to these results, all "pipistrelloid" genera, except *Eptesicus* and *Hesperoptenus*, share two derived features, i.e. rearranged chromosomes 15 and X. These species are thus considered to belong to two closely related tribes called Vespertilionini and Pipistrellini (VOLLETH 1989). The characteristic feature of the tribe Vespertilionini is the occurrence of state II of chromosome 11, differing from state I in a paracentric inversion. All Australian species examined so far (VOLLETH and TIDEMANN 1989, this paper) show the characteristics mentioned and belong therefore to the Vespertilionini, together with e.g. the European species *Vespertilio murinus* L., 1758 and *Hypsugo savii* (Bonaparte, 1837). Thus, representatives of three of HILL and HARRISON's (1987) *Pipistrellus* subgenera, i.e. *Hypsugo, Vespadelus* and *Falsistrellus*, fit in the tribe Vespertilionini, not in the Pipistrellini for karyological reasons. The often discussed (HELLER and VOLLETH 1984; KITCHENER et al. 1986; MENU 1987) polyphyletic origin of the genus *Pipistrellus* is thus confirmed. As a consequence, we propose the elevation of the subgenus *Vespadelus* to generic rank, as has been the case with *Hypsugo* and *Falsistrellus* (HORACEK and HANAK 1986; KITCHENER et al. 1986). However, the systematic position of the other species included in these taxa by HILL and HARRISON (1987) should remain tentative unless they have been examined cytogenetically. As far as the systematic position of *Falsistrellus* is concerned, our results corroborate the morphological analyses of KITCHENER et al. (1986). This genus is closely related to *Vespadelus*, sharing a common feature, the short arm on chromosome 7.

The classification of the genera *Nyctophilus* and *Scotorepens* with the Vespertilionini might be surprising at first view, because of their morphological specializations. However, it seems rather improbable that the chromosomal features mentioned, which arise through relatively rare events, i.e. inversions, should have evolved independently in two or three lineages in Australia.

In contrast to *Nyctophilus*, which possesses no chromosomal peculiarities, the karyotype of *Scotorepens* shows several special features. Among them are some which could be considered as being in common with the tribe Nycticeiini. The first is the acrocentric condition of some of the chromosomal arms 1 to 6. In the Nycticeiini, either none (e.g. *Scotophilus, Antrozous*, BICKHAM 1979b; RUEDAS et al. 1990) or one (*Nycticeius humeralis*, BICKHAM 1979b; *Rhogeessa alleni*, VOLLETH 1989) of the original three metacentrics (1/2, 3/4, 5/6) is conserved. In *Scotorepens balstoni*, however, the remaining metacentric element is chromosome 1/2 and not 3/4 as in *Nycticeius* and *Rhogeessa alleni*. The second feature concerns the NOR-bearing secondary constriction. Except for *Scotorepens*, chromosome 15 bears the NOR in all Australian species examined so far. In *Scotorepens balstoni*, however, the NOR is located on chromosome 23 and thus on the same

chromosome as in the American *Rhogeessa alleni* (VOLLETH 1989). Because it has been shown that the location of the Nucleolus Organizer Region has changed several times in the evolution of the vespertilionids (VOLLETH 1987), we consider this feature to have evolved independently in *Rhogeessa* and *Scotorepens*. The independent occurrence of such rare events as inversions is much more unlikely. In our opinion, the genus *Scotorepens* is a member of the Vespertilionini, which acquired the Nycticeiini-like morphological features through parallel evolution. This has also been proven to be the case with the semi-arid species *Otonycteris hemprichii*, which from a karyological point of view clearly belongs to the Plecotini (ZIMA et al. 1991), but was hitherto regarded as belonging to the Nycticeiini (see e.g. KOOPMAN 1984).

Without knowledge of the karyotype, nothing can be said about the phylogenetic relationships of *Scoteanax*. Morphometric and electrophoretic studies, however, revealed that *Scoteanax rueppellii* is not as closely related to *Scotorepens* as previously thought (KITCHENER and CAPUTI 1985; BAVERSTOCK et al. 1987).

Origin of the Australian vespertilionids

The bat fauna of Australia and New Guinea shows a high degree of endemism, with 54 % of Australian bats being endemic species (HALL 1984).

Within the family Vespertilionidae, 25 of the 34 known species are confined to Australia. And only 4 of them cover a range which extends beyond New Guinea (see Table 1).

Of the vespertilionid genera occurring in Australia and/or New Guinea, 50 % have an Asian or world-wide distribution. The remaining 50 % are distributionally restricted to Australia, New Zealand, New Guinea and some small islands in the area (see Table 1). 5 of

Table 1. **Distribution of Australian und New Guinean vespertilionid species**

		Number of endemic species			Non-endemic species[1]	
Genus	Distrib.[2]	Australia	NG	A + NG	A + NG	NG only
Pipistrellus	WW	2	1	–	–	3
Myotis	WW	–	–	–	1	–
Miniopterus	OW	–	–	–	2	4
Kerivoula	OW	–	1	–	–	–
Phoniscus	AA	–	–	1	–	–
Murina	AA	–	–	–	1	–
Philetor	AA	–	–	–	–	1
Nyctophilus	A, NG[3]	4	2	2	–	–
Pharotis[4]	NG	–	1	–	–	–
Chalinolobus	A, NG[5]	4	–	1	–	–
Falsistrellus	A	2	–	–	–	–
Vespadelus	A	9	–	–	–	–
Scotorepens	A	3	–	1	–	–
Scoteanax[4]	A	1	–	–	–	–

Data taken from: STRAHAN (1983), FLANNERY (1990), KITCHENER and CAPUTI (1985), KITCHENER et al. (1986, 1987).
[1] All non-endemic species found in Australia have also been discovered in New Guinea. – [2] Distribution of the genus: WW = worldwide; OW = Old World; AA = Asia plus Australia; A = Australia; NG = New Guinea. – [3] One *Nyctophilus* species (*N. heran*) recently discovered on Lembata I., Indonesia (KITCHENER et al. 1991); questionable type locality of *N. timorensis* is Timor, Indonesia. – [4] Karyological data not available. – [5] Range of *Chalinolobus gouldii* includes New Caledonia and Norfolk I. (TIDEMANN 1986); one endemic species (*Chalinolobus tuberculatus*) occurs in New Zealand.

these 7 genera have been examined karyologically (Volleth and Tidemann 1979, this paper) and all have been found to belong to the same tribe, Vespertilionini. This close relationship in addition to the limited distribution leads to the suggestion of a common origin for all Australian Vespertilionini. Furthermore, we assume that a long period of time was required for the evolution of this tribe, which resulted in bats occupying a wide range of adaptive niches, e.g. the highly manouverable foliage-cleaning *Nyctophilus*, or the genus *Scotorepens* some of which are capable of tolerating aridity. The first possibility of vespertilionids reaching Australia via Indonesia probably took place sometime in the Oligocene. At this time the ancestor of the Corvini (Aves) is thought to have moved in the opposite direction, from Australia to Asia (Sibley and Ahlquist 1985). Therefore, the immigration of a few bats during the same period seems to be possible. Under favourable circumstances even small bats seem to be able to cross wide stretches of ocean, as shown by the occurrence of *Chalinolobus tuberculatus* in New Zealand and of *Chalinolobus gouldii* in New Caledonia (Tidemann 1986).

Several points support the view that the remaining Australian vespertilionid species, coming from Asia, perhaps via New Guinea, reached Australia considerably later, probably not earlier than during the Pliocene. These species, in contrast to the members of the endemic genera, failed to colonize the whole continent, occurring only on the northern and eastern coasts of Australia. With the exception of two endemic species of *Pipistrellus*, which are thought to have evolved independently from Papuan forms (Kitchener et al. 1986), the remaining five Australian non-Vespertilionini species, belonging to four different subfamilies, also occur in New Guinea (see Tab. 1). In addition to *Phoniscus papuensis*, an endemic species of the Southeast-Asian genus, four widely distributed species (*Murina florium, Myotis adversus*, and two *Miniopterus* spp.) were successful in colonizing the region.

About the same extent of species exchange took place in the opposite direction, from Australia to New Guinea. *Chalinolobus nigrogriseus* and *Scotorepens sanborni* are thought to have reached New Guinea during the Pleistocene (Flannery 1990). Members of the genus *Nyctophilus*, however, must have reached New Guinea considerably earlier, probably during the Miocene (Flannery 1990). In addition to two species which inhabit both Australia and New Guinea, there are two *Nyctophilus* species and the related monotypic genus *Pharotis*, restricted to New Guinea. Furthermore, one recently described species, *Nyctophilus heran*, has been discovered on an Indonesian island (Kitchener et al. 1991), adding support to Timor as the hitherto questionable type locality of *Nyctophilus timorensis*. In addition to these biogeographic peculiarities, the distribution of an ectoparasitic mite genus provides further information. In contrast to the occurrence of the same *Pteracarus* species in the vespertilionid genera *Chalinolobus, Scotorepens* and *Vespadelus*, the mite species parasitic on *Nyctophilus* has not been found on any other genus (Fain and Lukoschus 1979). The morphological specializations found in *Nyctophilus* and *Pharotis*, their biogeographic relationships and the evolution of a specialized ectoparasite in *Nyctophilus* support the idea of an early branching of *Nyctophilus* from the Australian Vespertilionini stock.

Too few karyological features have been found to evaluate intergeneric relationships, other than that a close affinity between *Vespadelus* and *Falsistrellus* seems highly probable. In sum, 76 % (26 species) of the Australian vespertilionids are considered to be the result of the Vespertilionini radiation and only 24 % (8 species) are made up of other vespertilionid tribes and subfamilies.

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Zusammenfassung

Die phylogenetische Herkunft der australischen Vespertilioninae nach cytogenetischen Ergebnissen

Zwei australische Vespertilionidenarten, *Falsistrellus tasmaniensis* und *Scotorepens balstoni*, wurden cytogenetisch untersucht. Der Karyotyp von *Falsistrellus* besteht aus 44 Chromosomen und ist bis auf geringfügige Veränderungen mit dem anderer australischer Vespertilioninae identisch. Demgegenüber ist der Chromosomensatz von *Scotorepens balstoni*, der sich aus 30 Chromosomen zusammensetzt, stärker verändert.

Ein gemeinsames Merkmal aller bislang cytogenetisch untersuchten australischen Vespertilioninae ist ein verändertes Chromosom 11, das aufgrund einer vergleichenden Untersuchung zahlreicher anderer Gattungen (Volleth 1989) als abgeleitet zu betrachten ist. Aufgrund dieses Merkmals gehören die auf Australien und Neuguinea beschränkten Gattungen *Nyctophilus, Chalinolobus, Falsistrellus* und *Scotorepens* sowie die *Pipistrellus*-Untergattung *Vespadelus* alle derselben Tribus, Vespertilionini, an. Da jedoch andere Arten der Gattung *Pipistrellus* nicht zu dieser Tribus, sondern zu den Pipistrellini zu rechnen sind, wird die Anhebung des Taxons *Vespadelus* in den Rang einer Gattung vorgeschlagen. Die nahe Verwandtschaft der morphologisch sehr unterschiedlichen Gattungen weist, zusammen mit dem begrenzten Verbreitungsgebiet, auf die Abstammung von einem gemeinsamen Vorfahren und eine anschließende adaptive Radiation in Australien hin.

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Comparative cytogenetics of the Hyracoidea: chromosomes of two *Hyrax* species from South Africa

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Abstract

Described the chromosomes of the tree hyrax (*Dendrohyrax arboreus*: 2n = 54) and the yellow-spotted hyrax *(Heterohyrax brucei:* 2n = 54) from South Africa. Metaphase chromosomes were obtained from tissue culture and G-banding and C-banding patterns studied. Karyotypic comparisons between the species allowed for the identification of G-band homologies for most of the autosomes. The X chormosomes were identical in morphology and banding patterns, while the *D. arboreus* submetacentric Y chromosome differed from the acrocentric *H. brucei* counterpart by the addition of a heterochromatic short arm. While the C-band material is strictly centromeric in *H. brucei,* the tree hyrax, *D. arboreus,* is characterized by pronounced heterochromatic short arms in several of the chromosomes; terminal C-bands were also noted in some of the autosomes.

Introduction

The Hyracoidea is a distinctive order containing a single family, the Procaviidae, which is confined to Africa and the Arabian region (Corbet 1978). Although disputed since 1892, the consensus now appears that the family includes three distinct genera – *Procavia, Heterohyrax* and *Dendrohyrax* (Meester et al. 1986). In South Africa the rock hyrax, *P. capensis,* occurs widely though limited to suitable rocky habitat. In contrast, the distribution patterns of the two species which form the subject of this report, *D. arboreus* and *H. brucei*, are restricted in South Africa. The yellow-spotted hyrax, *H. brucei,* occurs only in the extreme northeastern parts of the country but extends through Zimbabwe, parts of Mozambique and Botswana, northwards through central and eastern Zambia, Malawi, Tanzania, Kenya, Uganda, Somalia and southern and southwestern Sudan. The tree hyrax, *D. arboreus,* classified in the South African Red Data Book as rare due to habitat destruction (Smithers 1986), is limited to pockets of indigenous forest in the south-eastern Cape Province and the Natal midlands and has been recorded from parts of Mozambique, Malawi, Zambia, Zaire, Tanzania, Kenya and Uganda. The species is replaced in eastern Tanzania and its offshore islands by *D. validus* and, in the forests of the Congo Basin and west Africa, by *D. dorsalis*, both of which are closely allied species (Smithers 1983).

Published karyotypic data on the Hyracoidea are restricted to unbanded preparations of the ubiquitous *P. capensis* (2n = 54; Hungerford and Snyder 1969; Hsu and Benirschke 1971b). In the present report, we detail the G-banding and C-banding patterns of two, hitherto unreported, hyrax species. Our data, together with those published on *Procavia*, suggest an ancestral diploid number of 2n = 54 for the family. Furthermore, at least in respect of the species covered by this report, karyotypic evolution has proceeded largely through complex chromosomal rearrangements that appear to have disrupted G-band homology in some autosomes and through changes in the distribution of constitutive heterochromatin.

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Material and methods

Number of specimens studied from each species, the sample localities and their approximate grid references are presented below.

Dendrohyrax arboreus: 1 male – Pirie Forest, eastern Cape Province (32° 46′ S, 29° 21′ E).

Heterohyrax brucei: 2 males – Blyde River Nature Reserve (24° 39′ S 30° 50′ E) and Vhembi Nature Reserve (22° 12′ S, 29° 21′ E).

Skins and skulls from each study animal (excluding the *H. brucei* specimen from Blyde River which was badly damaged) have been deposited as voucher specimens in the mammal collections of the Kaffrarian and Transvaal Museums.

Metaphase chromosomes were obtained from fibroblast cultures which were initiated from ear biopsies and maintained in McCoy 5A medium supplemented with 10 % fetal calf serum. Chromosomes were G-banded and C-banded following the methods of Wang and Fedoroff (1972) and Sumner (1972) respectively. The diploid chromosome number was determined by counting 25 cells from each specimen while chromosome measurements were taken directly from photographs using a Quantimet 520 Image Analyzer (Cambridge Instruments, UK). The G-banded karyotype of each species was standardized based on the percentage contribution of each chromosome to the female genome (Lee and Martin 1980). Chromosomes were grouped by establishing chromosome arm ratios (metacentric 1.0–1.1; submetacentric 1.1–1.9; subtelocentric > 2; acrocentric with no visible short arm; Levan et al. 1964) and ordered in decreasing size. In the case of *D. arboreus,* one autosomal pair, pair 6, was characterized by marked heteromorphism. The submetacentric morph differed from its acrocentric homolog by the presence of additional heterochromatin in the short arm. Consequently, in standardizing this species karyotype, we have chosen to exclude the heterochromatic short arm of the submetacentric morph; therefore length measurements of this pair merely represent the acrocentric morphology.

Results

Both *D. arboreus* and *H. brucei* are characterized by 2n = 54 which, when taken together with the published data on *P. capensis,* reflect the conserved nature of the diploid number across the three extant hyrax genera. The G-banded karyotype of *D. arboreus* is shown in Figure 1 and the chromosomes numbered and standardized based on the percentage contribution of each to the genome (Tab. 1).

The autosomal chromosome complement of *D. arboreus* comprises 15 acrocentric pairs (1–15, one of which, pair 6, shows pronounced heteromorphism), five pairs of subtelocentric autosomes (16–20), five pairs of submetacentric (21–25) and one pair of metacentric

Table 1. **Relative chromosome lengths of *Dendrohyrax arboreus* expressed as a percentage of the haploid female karyotype (n=4)**

Chromosome number	Relative length % of (A+X) x	SE	Chromosome number	Relative length % of (A+X) x	SE
1	5.212	0.076	15	2.056	0.069
2	5.038	0.112	16	6.417	0.154
3	4.944	0.127	17	4.896	0.129
4	4.424	0.171	18	4.598	0.059
5	4.292	0.159	19	3.658	0.042
6	3.238	0.057	20	3.541	0.071
7	3.587	0.114	21	3.475	0.086
8	3.572	0.212	22	3.345	0.098
9	3.428	0.037	23	2.712	0.030
10	3.332	0.091	24	2.705	0.065
11	3.322	0.092	25	2.249	0.100
12	2.822	0.049	26	1.985	0.054
13	2.529	0.163	X	4.938	0.145
14	2.351	0.045	Y	1.955	0.108

x = arithmetic mean; SE = standard error.

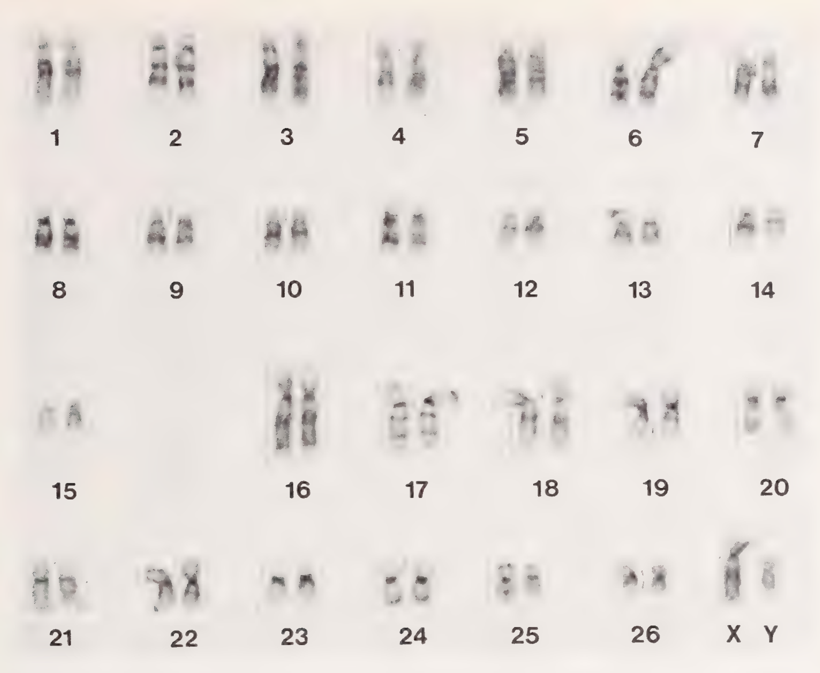


Fig. 1. G-banded karyotype of a male tree hyrax, *Dendrohyrax arboreus* (2n = 54). The heteromorphism evident in the lengths of the p arms of the homologs constituting pair 6 is attributable to differences in heterochromatin

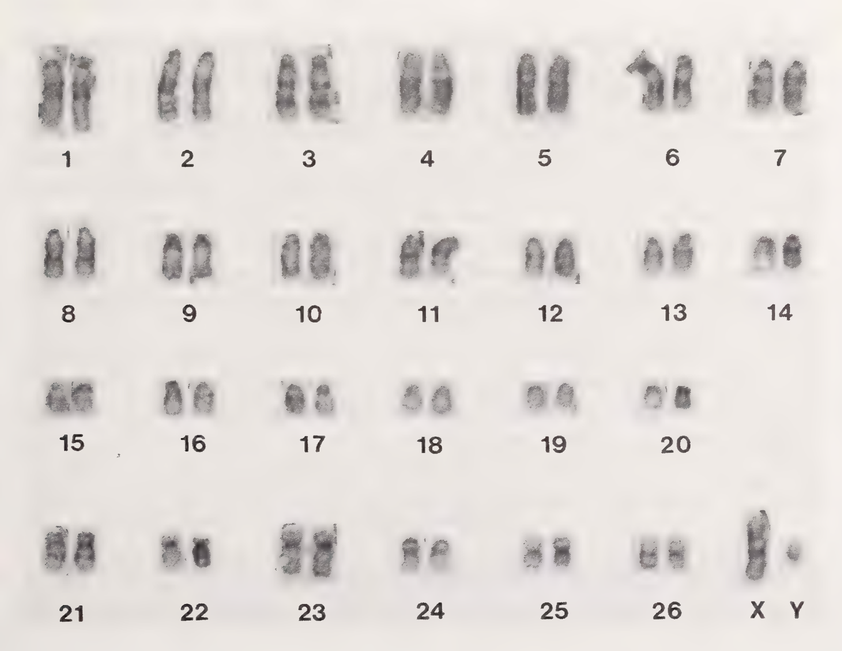


Fig. 2. G-banded karyotype of a male yellow-spotted hyrax, *Heterohyrax brucei* (2n = 54)

Table 2. **Relative chromosome lengths of *Heterohyrax brucei* expressed as a percentage of the haploid female karyotype (n=4)**

Chromosome number	Relative length % of (A+X) x	SE	Chromosome number	Relative length % of (A+X) x	SE
1	6.588	0.166	15	2.770	0.151
2	6.010	0.200	16	2.560	0.073
3	5.732	0.159	17	2.449	0.083
4	5.360	0.279	18	2.145	0.104
5	5.226	0.120	19	2.119	0.038
6	4.748	0.157	20	1.972	0.091
7	4.400	0.115	21	3.353	0.085
8	4.257	0.066	22	2.796	0.058
9	3.916	0.108	23	4.027	0.047
10	3.865	0.097	24	2.713	0.052
11	3.774	0.067	25	2.548	0.061
12	3.240	0.030	26	2.327	0.084
13	3.034	0.041	X	5.199	0.130
14	2.884	0.054	Y	1.350	0.166

x = arithmetic mean; SE = standard error.

chromosomes (26). The X chromosome is the largest submetacentric chromosome and constitutes 5 % of the female haploid complement; the submetacentric Y is intermediate in size between pairs 25–26 forming approximately 2 % of the female genome (Tab. 1).

The *H. brucei* karyotype (Fig. 2) has 20 acrocentric autosomal pairs (1–20), two subtelocentric autosomal pairs (21–22), two submetacentric (pairs 23–24) and two metacentric autosomal pairs (25–26). The X chromosome is the largest submetacentric chromosome in the complement and contributes 5.2 % to the female genome, while the acrocentric Y, due to its small size, is readily distinguishable even in unbanded preparations and constitutes 1.4 % of the haploid genome (Tab. 2).

A comparison of the G-banded chromosomes of the two hyrax species is shown in Figure 3. Convincing G-band homology is clearly evident for the euchromatic portions of the majority of chromosomes including the X which shows two dark bands in the middle of the long arm which are characteristic for most mammals (Pathak and Stock 1974). The only exceptions to this are chromosomes 4, 9, 17–19, and 21 in the *Dendrohyrax* karyotype and 9–10, 15, 17, 19, and 20 in *Heterohyrax.* In determining homologies between these species it is also informative to compare the relative amounts and distribution of constitutive heterochromatin present in their genomes. In *H. brucei* the distribution of C-band material is strictly centromeric while the *D. arboreus* karyotype is characterized by several of the autosomes having pronounced heterochromatic short arms and blocks of terminal heterochromatin (Fig. 4A and B). This difference has led to the length discrepancies evident in the comparison of the G-banded chromosomes of the species and is most pronounced in respect of their Y chromosomes as well as *Dendrohyrax* chromosome 6 cf *Heterohyrax* 7, *Dendrohyrax* 7 cf *Heterohyrax* 8, *Dendrohyrax* 16 cf *Heterohyrax* 2 and *Dendrohyrax* 22 cf *Heterohyrax* 16.

Discussion

The Hyracoidea are a group of phenotypically similar herbivorous mammals (also known as "dassies" and sometimes referred to as "conies") whose distribution is Afro-Arabian and whose origins, based on the fossil record, are strictly African (De Blaise and Martin 1982). The terrestrial forms (*Procavia* and *Heterohyrax*) live in colonies while *Dendro-*

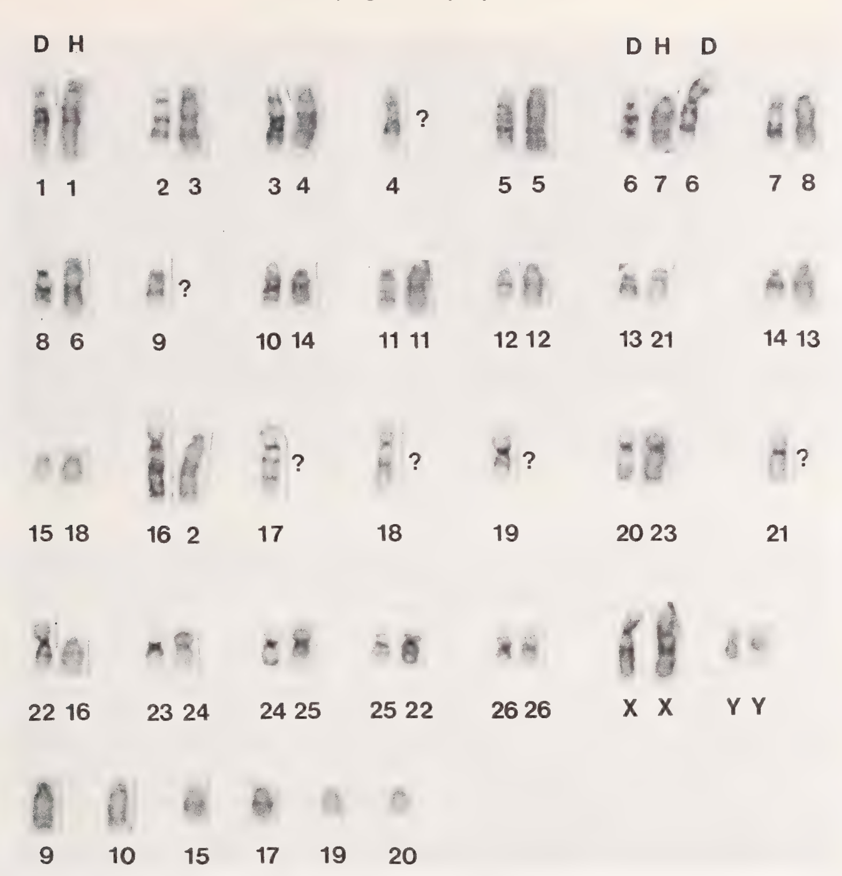


Fig. 3. Comparison of the G-banded chromosomes of *Dendrohyrax arboreus* (D) and *Heterohyrax brucei* (H). The first chromosome in each pair is that of *Dendrohyrax*. Both chromosome 6 morphs detected in the *D. arboreus* specimen are matched to the *H. brucei* counterpart. Unmatched chromosomes in the *D. arboreus* karyotype are indicated by (?), while the acrocentric elements at the bottom of the figure are of *H. brucei*

hyrax, although not showing any obvious limb modifications, is arborial and not gregarious (Smithers 1983). Since cytogenetic rearrangements which characterize chromosomal evolution are thought to reach fixation through small effective population size (Bentsson and Bodmer 1976; Bush et al. 1977; Lande 1979), it is not unreasonable to anticipate that those species whose habitat specificity predisposes them to population fragmentation may be characterized by variation in karyotype – a situation which could hold for the Hyracoidea. For example, *Heterohyrax* like *Procavia* inhabits "koppie" habitat typically comprising jumbled boulders and rocky outcrops which is often discontinuous, resembling terrestrial islands, with limited opportunity for gene flow between populations. Likewise, the tree hyrax's (*Dendrohyrax*) dependency on developed woodland and forest could similarly predispose it to population fragmentation.

Given evidence of a conserved diploid number of 2n = 54 in representative species of all three extant genera, we propose that the ancestral Hyracoidea was characterized by this chromosome number although, it should be noted, commonality does not always necessarily imply the primitive condition (Qumsiyeh and Baker 1988). However, should this hypothesis hold, karyotypic evolution in the Hyracoidea has obviously not proceeded by

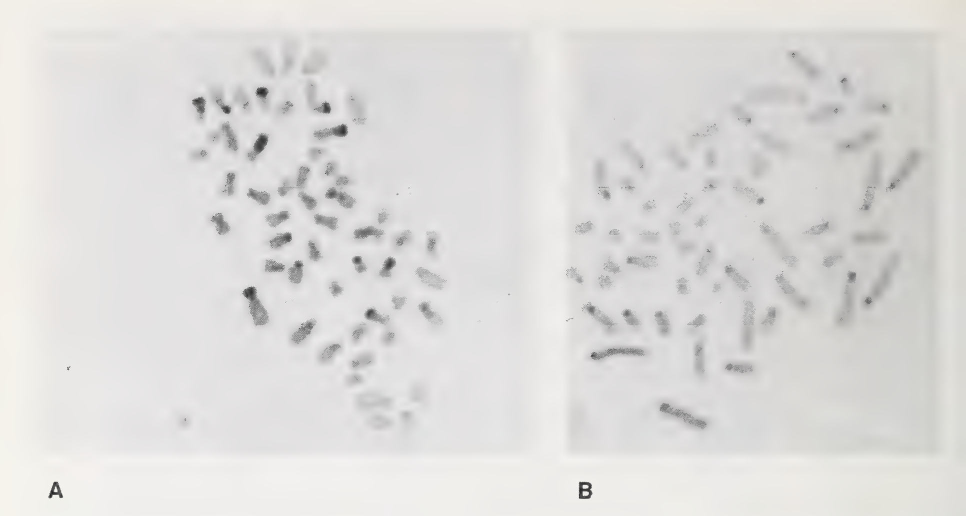


Fig. 4. C-banded metaphase cells of *Dendrohyrax arboreus* (A) and *Heterohyrax brucei* (B). Note the presence of heterochromatic short arms in several of the *D. arboreus* chromosomes (as well as the telomeric blocks of C-positive material in certain instances)

structural changes which involve fusions of chromosomes or chromosome arms. As is evident from the comparative cytogenetic data contained herein, the failure to identify corresponding homologs for several autosomes of the *D. arboreus* and *H. brucei* karyotypes would seem to suggest that, instead, karyotypic evolution has probably progressed through paracentric inversions and reciprocal translocations, both categories of chromosomal change that would disrupt G-band sequence homology.

Of particular interest are the marked differences that exist in the distribution of constitutive heterochromatin in the *H. brucei* and *D. arboreus* karyotypes. While the former has small amounts of strictly pericentromeric heterochromatin, the *D. arboreus* genome is characterized both by the presence of entirely heterochromatic short arms (for example pair 6) as well as terminal bands of heterochromatin in several of the autosomal pairs (Fig. 4 A). C-banding is thought to stain genetically inert blocks of DNA (John and Miklos 1979) and, for this reason, often shows intraspecific and intra-individual variability (for example Ward et al. 1987; Matayoshi et al. 1987; Robinson and Elder 1987). However, chromosomal position (terminal, interstitial or centromeric) of C-positive material occasionally differs between species and has been used in a cladistic framework (van Tuinen and Ledbetter 1983; van Tuinen and Valentine 1986). This contrast in C-band patterns between *D. arboreus* and *H. brucei* raises the possibility that, following analysis of other hyrax species, C-banding may be a particularly useful cytogenetic adjunct in ascertaining synapomorphies for this group.

In conclusion, although cytogenetic data are currently sparse for the Hyracoidea, it is quite possible that interspecific variation in the euchromatic and heterochromatic portions of the genome may exist beyond the confines of the species analyzed in this study. Future comparisons both within the Hyracoidea, as well as with a representative Subungulate outgroup (for example the elephant, *Loxodonta africana* 2n = 56; Hsu and Benirschke 1971a), may shed light on the phylogenetic relationships of this primitive mammalian assemblage.

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Zusammenfassung

Vergleichende Cytogenetik der Hyracoidea: Chromosomen von zwei Schliefer-Arten aus Südafrika

Die Karyogramme der beiden Schliefer-Arten (Procaviidae) *Dendrohyrax arboreus* (2n = 54) und *Heterohyrax brucei* (2n = 54) zeigten weitgehende Übereinstimmung in den G-Banden der Autosomen und der X-Chromosomen. Offenbar infolge zu großer struktureller Veränderungen ließen sich aber einige Chromosomen nicht homologisieren. Die Lokalisation des konstitutiven Heterochromatins auf den Chromosomen ist bei den beiden Arten unterschiedlich: bei *H. brucei* sitzt es am Zentromer, während bei *D. arboreus* ganze kurze Arme von Chromosomen heterochromatisch sind oder das C-positive Material endständig ist.

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Fangmethoden und Geschlechterverhältnis in Stichproben von Feldmauspopulationen, *Microtus arvalis* (Pallas, 1779)

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Abstract

Sex ratio of Microtus arvalis (Pallas, 1779) – samples caught in different types of traps

Studied the sex ratio of *Microtus arvalis,* collected east of Vienna from 1981 to 1987 in pitfalltraps (70615 trapnights, 6547 voles) and in snaptraps (9386 trapnights, 1055 voles). The unbaited pitfalls were set in different habitats of agricultural areas, in fields near settlements and in fields in riverside forests. The snaptraps (bait: soft cheese or margarine) were set on road-sides along open fields and in extensively cultivated meadows in riverside forests.

In accordance with literature, females predominate in snaptraps. In pitfalls males outnumber females statistically significant from March to July; later no sexual bias is noted. When one of the sexes predominates, it correlates to the proportion of sexually active males (testes > 130 mg) to pregnant females. Such males seem to be more mobile and not to be attracted very strongly by bait. Thus, they were caught on a large scale in pitfalls. Pregnant females seem to be forced into mobility by their higher requirement for nourishment and to be attracted by the bait of snaptraps. The abundance of the voles does not affect these findings.

Mutual elimination of males influences sex ratio in pitfalls after July as well as in snaptrap-catches, but seems to play a role already earlier, as a size analysis indicates.

Einleitung

Das Geschlechterverhältnis ist ein sehr wesentlicher demökologischer Parameter, dessen Dynamik bei *Microtus arvalis* viel Beachtung gefunden hat. Es wird meist als gesichert angenommen, daß erstens zur Fortpflanzungszeit die Weibchen dazu tendieren in Stichproben zu überwiegen, und daß sich zweitens die geschlechtsaktiven Männchen gegenseitig umso mehr eliminieren, je höher die Dichte ist („Männchenelimination"). Diese Befunde beruhen auf Schlagfallenfängen (z. B. Stein 1953), Stichproben aus ausgegrabenen Bauen (Stein 1957) oder der Geschlechtsbestimmung an Beckenknochen aus Eulengewöllen (Becker 1954). Niethammer und Krapp (1982) übernehmen diese Ergebnisse. Barberfallenfänge von Dub (1971) und Götz (in Somsook 1990) widersprechen den angeführten Meinungen insofern, als sie ein Überwiegen von Männchen ergeben. Vorliegende Arbeit basiert auf dem Material der Dissertation von Somsook (1990).

Material und Methoden

Götz (1991) sammelte von März 1981 bis Februar 1982 Kleinsäuger in unbeköderten und stationären Barberfallen. Diese waren in verschiedenen Sonderstandorten (ein Restwäldchen, eine Mähwiese und Windschutzstreifen) und Ackerkulturen des offenen Marchfeldes sowie in siedlungsnahen Äckern am Stadtrand von Wien und in weiteren Ackerflächen, die im nahen Donau-Auwald eingesprengt sind, eingesetzt (58.455 Falleneinheiten, 6.302 Feldmäuse). Ferner setzte er diese Fänge in reduziertem Umfang, nämlich in einem Windschutzstreifen und in einem Weizenfeld auch 1982 und 1983 fort (12.160 Falleneinheiten und 245 Feldmäuse). Schließlich waren im Sommer 1981 an zwei vergleichbaren Weizenfeldrändern, an dem einen 10 Schlagfallen und am anderen gleichviele Barberfallen synchron im Einsatz (je 300 Falleneinheiten; 49 bzw. 414 Feldmäuse). H. Götz stellte uns das genannte Material für detaillierte populationsdynamische Analysen zur Verfügung.

1981 trat im offenen Ackerland ein Dichtemaximum auf, 1982 und 1983 herrschte nach einem

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Zusammenbruch niedere Dichte und bis 1987 gab es im Gebiet keine weitere Übervermehrung. In diesem Jahre untersuchten wir mittels Köder, der mit farbigen Wollfasern markiert war (Methode nach Holišova 1968) und anschließenden Schlagfallenfängen in monatlichen Abständen (April bis Oktober) die Mobilität der Feldmaus. Dies geschah synchron an Straßenböschungen im offenen Marchfeld und an den Böschungen des Hochwasserschutzdammes der Donau im Auwald (je 2.700 Falleneinheiten, 384 bzw. 181 Feldmäuse). Zusätzlich fing Somsook mittels Schlagfallen (3.686 Falleneinheiten) auf Auwiesen weitere 441 Feldmäuse (Somsook und Steiner 1991). Steiner fing in den Auwäldern der Donau in den Jahren 1956–1974 mit verschiedenen Fangmethoden 117 Feldmäuse.

Das Marchfeld war bis zur Donauregulierung eine Überschwemmungsebene nordöstlich von Wien, die heute nur mehr geringe Waldreste und fast keine Wiesen besitzt. Sie ist intensiv ackerbaulich genutzt. Im Süden grenzen heute noch Donau-Auen an.

Die Feldmäuse wurden nach den üblichen Methoden vermessen und seziert. Als geschlechtsaktiv wurden Männchen mit einem Hodengewicht von mindestens 130 mg (eingefrorenes Material, Pelikán 1959) bzw. ab 90 mg (in Alkohol fixierte Fänge) betrachtet. Weibchen mit Embryonen wurden ebenfalls als aktiv angesehen (Somsook 1990). Abweichungen vom ausgeglichenen Geschlechterverhältnis 50:50 wurden mit dem Chi-Quadrat-Test auf Signifikanz geprüft.

Ergebnisse

In allen mit Hilfe von Barberfallen erzielten Gesamtfängen überwiegen die Männchen (Abb. 1). Besonderes Gewicht haben die über ein ganzes Jahr (von März 1981 bis Februar 1982) laufenden Fänge in drei verschiedenen Ackergebieten: Die Prozentanteile der Männchen schwanken hier zwischen 56,7 und 61,5 %; der Unterschied zu einem 1:1-Verhältnis ist jeweils bei einer Irrtumswahrscheinlichkeit unter 1 % signifikant. Diese Fänge fielen in ein Jahr mit Dichtemaximum und nachfolgendem Zusammenbruch. Von dem in einem Weizenfeld und in einem Windschutzstreifen 1982 und 1983 erbeuteten Material ist in Abb. 1 bloß jenes von März bis August dargestellt. Dem Zusammenbruch entsprechend ging der Fang stark zurück (1981: 483; 1982: 78; 1983: 135 Ex.). Die

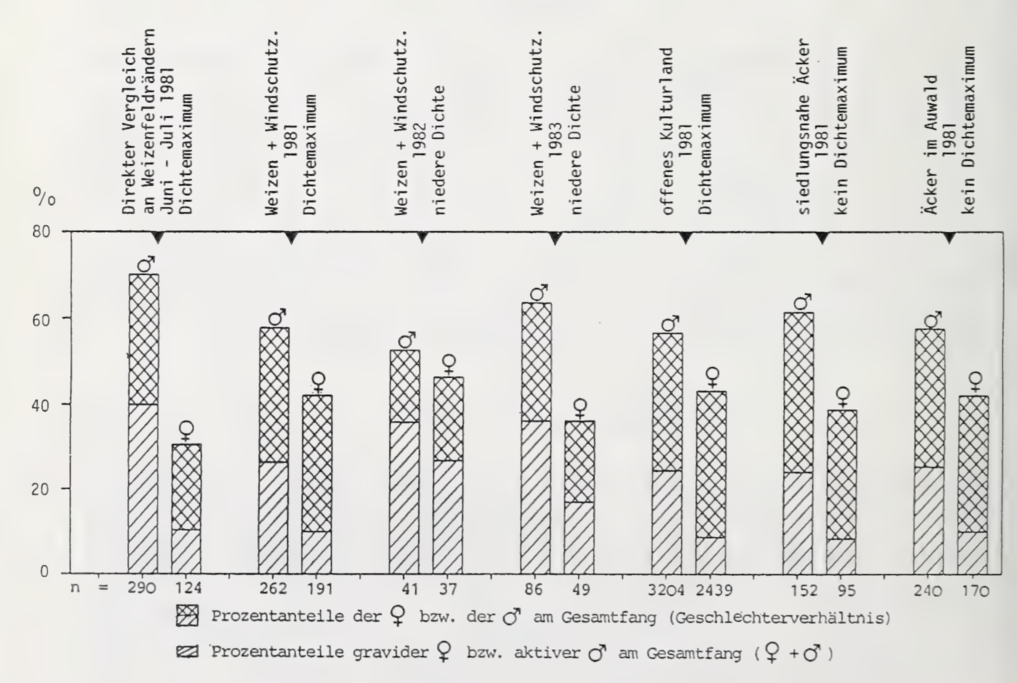


Abb. 1. Geschlechtsaktivität und Geschlechterverhältnis in Barberfallenfängen

Abweichung vom Verhältnis 50:50 war 1981 und 1983 auf dem 1-%-Niveau signifikant. Ein direkter und synchroner Vergleichsfang an Weizenfeldrändern über 30 Tage (zur Zeit erhöhter Dichte im Jahr 1981) ergab bei den Barberfallenbeuten ein signifikantes Überwiegen von Männchen (70 %).

Deutlich verschieden ist das Bild bei den Schlagfallenfängen (Abb. 2): Im eben zitierten Vergleichsfang stellen die Weibchen 73,5 % bei einem Materialumfang von nur 49 Tieren. Die Fänge von Straßenböschungen im offenen Ackerland bzw. von Dammböschungen und Wiesen im Augebiet aus dem Jahre 1987 sind etwas umfangreicher. Die Weibchen überwiegen darin signifikant mit 62,6 bzw. 55,9 %. Eine kleine Serie von 117 in Waldlebensräumen der Auen gefangenen Feldmäusen (1956–1974 aus insgesamt ca. 7.000 Kleinsäugern, gesammelt von Steiner) zeigt ein ausgeglichenes Geschlechterverhältnis.

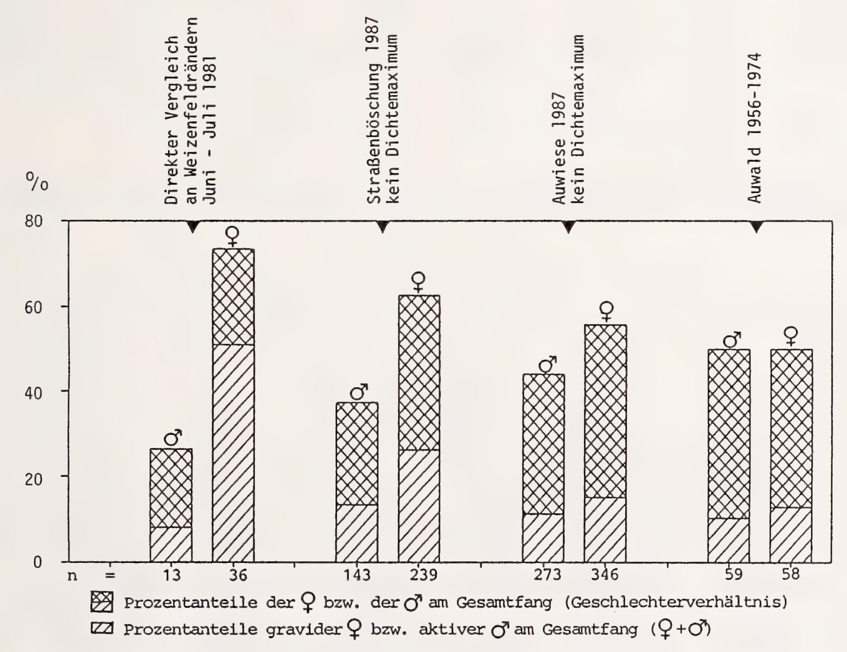


Abb. 2. Geschlechtsaktivität und Geschlechterverhältnis bei den Schlagfallenfängen (1981 und 1987) bzw. Fängen mittels verschiedener Methoden (1956–74)

Das umfangreiche Barberfallenmaterial des offenen Ackerlandes aus dem Jahr 1981 erlaubt eine Betrachtung nach Fangmonaten (Abb. 3): Bis zum Juli liegen die Männchenanteile über 50 %, Signifikanz ist gegeben im März, Juni und Juli (1-%-Niveau) bzw. Mai (5-%-Niveau). Von August bis Oktober sind die Anteile ausgeglichen. Das Schlagfallenmaterial von Straßenböschungen des gleichen Gebietes aus dem Jahr 1987 ist ungleich kleiner. In allen Monaten überwiegen die Weibchen. Nur für September und Anfang Oktober kann dieser Unterschied bei einer Irrtumswahrscheinlichkeit von 1 % statistisch abgesichert werden (Abb. 4).

Die weitere Analyse der Stichproben ergab, daß das Geschlechterverhältnis vor allem vom Anteil sexuell aktiver Tiere abhängt. Die diesbezüglichen Daten sind den Abb. 1–4 zu entnehmen. Bei den Weibchen konnten wegen z. T. unvollständiger Angaben bei Material, das aus mit Formol beschickten Fallen stammt, nur die graviden Tiere gewertet werden. Bei den Gesamtstichproben, sowohl aus Barberfallen als auch aus Schlagfallen, unterscheiden sich die Anteile nicht geschlechtsaktiver Männchen bzw. Weibchen auch dann nur

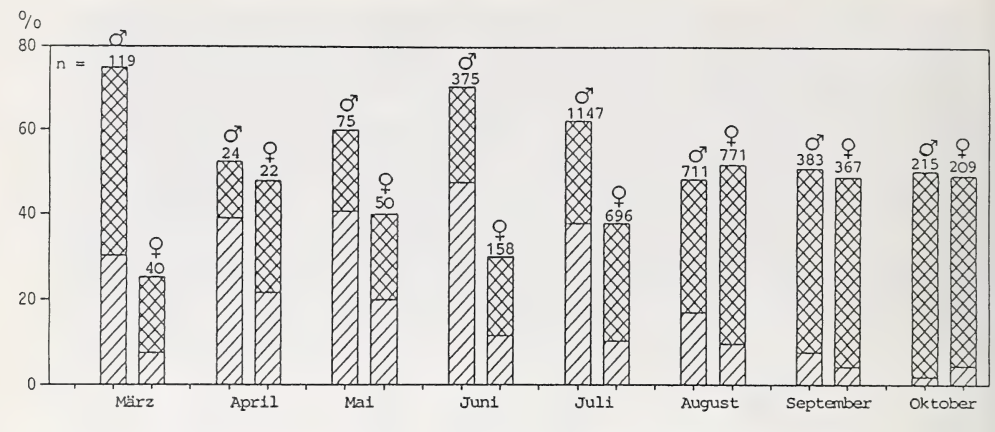


Abb. 3. Geschlechtsaktivität und Geschlechterverhältnis in Barberfallenfängen des offenen Ackerlandes von März bis Oktober 1981

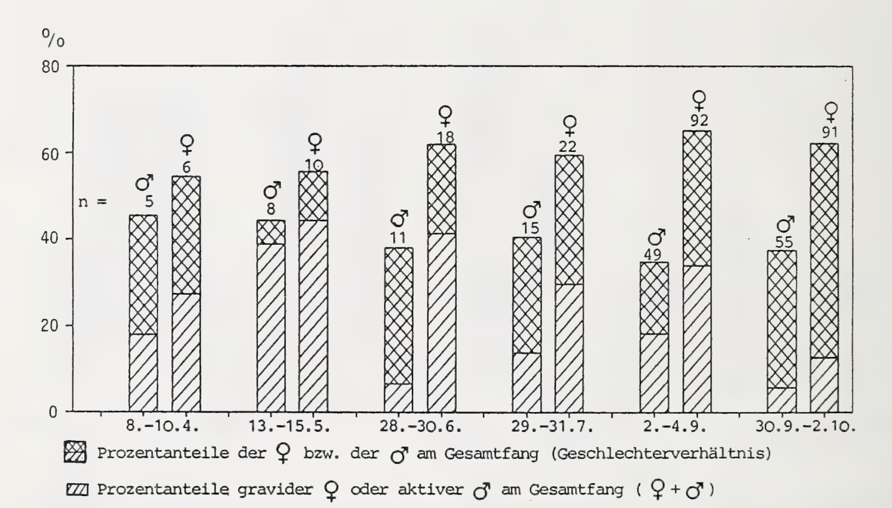


Abb. 4. Geschlechtsaktivität und Geschlechterverhältnis in Schlagfallenfängen des Jahres 1987, Straßenböschungen

wenig, wenn das Geschlechterverhältnis signifikant von der 1:1-Relation verschieden ist. Das bedeutet, daß für signifikant erhöhte Prozentanteile eines Geschlechtes vor allem der Anteil der aktiven Individuen ausschlaggebend ist.

So sind z. B. in den Vergleichsfängen von den Weizenfeldrändern (1981) bei den Barberfallen viermal mehr aktive Männchen (40 % des Gesamtfanges!) als gravide Weibchen gefangen worden (Abb. 1). In allen Stichproben mit signifikant verschiedenem Geschlechterverhältnis sind zwei- bis dreimal so viele aktive Männchen als gravide Weibchen. Nur 1982, bei sehr geringer Dichte, sind entsprechende Verhältnisse lediglich angedeutet. Dies bedeutet, daß auch in Ackerbereichen, in denen 1981 keine Massenvermehrung stattfand, die signifikant erhöhten Männchenanteile auf die überproportional

angewachsenen Zahlen aktiver Tiere zurückführbar sind. Für die Schlagfallenausbeuten gilt ähnliches mit umgekehrten Vorzeichen: je weiter sich der Weibchenanteil über die 50-%-Marke hebt, desto deutlicher ist dies vom Anteil gravider Individuen verursacht (Abb. 2).

Aus Materialgründen kann die jahreszeitliche Entwicklung dieser Verhältnisse nur in den Barberfallenfängen von 1981 genauer betrachtet werden (Abb. 3). Die Anteile aktiver Männchen sind auch in diesem Falle entscheidend: Sie sind bis zum Juli zwei- bis über viermal höher als die gravider Weibchen; nur im April (geringes Material, kein signifikantes Abweichen von der 1:1-Relation) sind es bloß 1,8mal mehr aktive Männchen. Ab August sind die Geschlechterverhältnisse ausgeglichen. Im August ist der Anteil aktiver Männchen noch etwa doppelt so hoch wie der der Weibchen. Im Prinzip ist die gleiche Entwicklung, aber in bezug auf Weibchen, auch in den Schlagfallenfängen (Abb. 4) zu erkennen.

Schließlich ist noch zu untersuchen, wie das Geschlechterverhältnis in verschiedenen Altersgruppen ist. Bei der Feldmaus darf dafür nur mit großen Vorbehalten die Condylobasallänge (CBL) herangezogen werden. Tabelle 1 zeigt das Barberfallenmaterial aus den

Tabelle 1. **Prozentuelle Männchen- und Weibchenanteile im Gesamtmaterial aus dem offenen Kulturland im Jahr 1981, aufgeschlüsselt nach Größenklassen der Condylobasallänge**

Barberfallenfänge

CB-Länge Klassen	Männchen n	Männchen %	Weibchen n	Weibchen %	Verhältnis ♂ : ♀	Chiquadrat-Test
−19,9	257	43,6	333	56,4	1:1,3	++
−20,9	216	36,4	377	63,6	1:1,7	++
−21,9	446	43,8	572	56,2	1:1,3	++
−22,9	920	68,4	426	31,6	2,2:1	++
−23,9	771	70,9	316	29,1	2,4:1	++
−24,9	320	51,8	298	48,2	1,1:1	−
≧ 25,0	231	67,3	112	32,7	2,1:1	++
Summe/$\bar{x}$	3161	56,4	2434	43,6	1,3:1	++

++ = Signifikante Abweichung vom Verhältnis 1:1 auf 1-%-Niveau; − = Unterschied nicht signifikant.

offenen Ackergebieten des Jahres 1981, aufgeschlüsselt nach der Größe und dem Geschlechterverhältnis. Bei Tieren unter 22,0 mm CBL überwiegen die Weibchen signifikant, bei größeren jedoch immer die Männchen. Ab dieser Grenze traten 1981 beide Geschlechter verstärkt in die Fortpflanzungstätigkeit ein (Somsook 1990). Nur in der Größenklasse von 24,0–24,9 mm Condylobasallänge ist der Männchenüberschuß so gering, daß er statistisch nicht absicherbar ist.

Tabelle 2 stellt die Schlagfallenfänge aus dem Jahre 1987 und dem selben Gebiet zusammen. Der Materialumfang ist gering. In den beiden Größenklassen unter 21 mm CBL liegt der Männchenanteil (statistisch nicht abgesichert) unter 50 %. 1987 begannen beide Geschlechter bereits ab dieser Größe in erhöhtem Maße an der Fortpflanzung teilzuhaben (Somsook 1990). Bis 24 mm CBL liegt der Prozentanteil der Männchen zwischen 16,1 und 32,7 (Irrtumswahrscheinlichkeit unter 1 %). Der geringen Endgröße der Weibchen entsprechend haben diese über 25 mm CBL nur mehr sehr geringen Anteil.

Tabelle 2. **Prozentuelle Männchen- und Weibchenanteile im Gesamtmaterial von den Straßenböschungen des offenen Kulturlandes im Jahr 1987, aufgeschlüsselt nach Größenklassen der Condylobasallänge**

Schlagfallenfänge

CB-Länge Klassen	Männchen n	Männchen %	Weibchen n	Weibchen %	Verhältnis ♂ : ♀	Chiquadrat-Test
−19,9	27	45,8	32	54,2	1:1,2	–
−20,9	20	47,6	22	52,4	1:1,1	–
−21,9	8	26,7	22	73,3	1:2,8	+
−22,9	17	32,7	35	67,3	1:2,1	+
−23,9	9	16,1	47	83,9	1:5,2	++
−24,9	12	36,4	21	63,6	1:1,8	–
≧25,0	14	87,5	2	12,5	7:1	++
Summe/$\bar{x}$	107	37,2	181	62,8	1:1,7	++

Signifikante Abweichung vom Verhältnis 1:1: ++ = $P<0.01$; + = $P<0.05$; – = Unterschied nicht signifikant.

Diskussion

In allen mit Schlagfallen erbeuteten Stichproben überwiegen die Weibchen, gleichgültig ob sie aus einzelnen Monaten oder längeren Zeiträumen stammen. Bei Proben von über 100 Tieren ist dieses Überwiegen statistisch gesichert (Ausnahme: Fänge aus dem Wald). Dies stimmt mit den Angaben in der Literatur überein (vgl. z. B. Niethammer und Krapp 1982). Je höher der Weibchenanteil ist, desto mehr wird deutlich, daß dafür die zunehmend große Zahl gravider Individuen verantwortlich ist (Abb. 2 und 4).

Völlig anders ist das Bild im Material aus Barberfallen (Abb. 1 und 3): In allen Proben, die während eines ganzen Jahres gesammelt wurden (offenes Kulturland, siedlungsnahe Äcker bzw. Äcker im Auwald 1981/82), aus dem Sommerhalbjahr stammen (Weizen und Windschutzstreifen 1981–1983) oder in einzelnen Monaten vor dem August gefangen wurden, überwiegen die Männchen. Von 12, sich teilweise ein wenig überlappenden Stichproben, sind 9 auf dem 1-%-Niveau und eine bei 5 % Irrtumswahrscheinlichkeit vom 50:50-Verhältnis verschieden. Dieser Unterschied beruht auch bei zunehmendem Männchenanteil immer deutlicher auf dem Anteil geschlechtsaktiver Tiere. Im August, vor dem Zusammenbruch der Population, überwiegen die Weibchen ein wenig, jedoch sind fast doppelt soviele geschlechtsaktive Männchen wie gravide Weibchen im Fang.

Es zeigt sich also, daß das Geschlechterverhältnis, das während der Fortpflanzungszeit festgestellt wird, vorwiegend durch das unterschiedliche Verhalten sexuell aktiver Männchen und gravider Weibchen bestimmt wird. Das Überwiegen trächtiger Weibchen in Schlagfallenfängen scheint durch ihren erhöhten Nahrungsbedarf zur Vermehrungszeit zu Stande zu kommen. So könnte ihr höherer Fanganteil in beköderten Fallen (bezüglich Feldmausfängen in Lebendfallen gibt z. B. Reichstein 1964 eine Relation von 485 Weibchen:376 Männchen an) erklärt werden. Die Mobilität fortpflanzungsaktiver Feldmausweibchen ist entgegen der allgemein geltenden Meinung höher als die ebensolcher Männchen (Somsook und Steiner 1991). Für die Rötelmaus (*Clethrionomys glareolus* Schreber, 1780) konnten Andrzejewski und Babinska-Werka (1986) zeigen, daß fortpflanzungsaktive Weibchen größere Aktionsräume haben als aktive Männchen. Sie werden offensichtlich auch stärker durch den Köder angelockt. Trojan und Wojciechowska (1967) und Grundwald (1975) unterstreichen die Bedeutung des Köders beim Fang der Feldmaus. So ist auch erklärlich, daß in Schlagfallen in den Größenklassen der Condylobasallänge 21–24 mm die Weibchen am deutlichsten überwiegen. Ab 24 mm, besonders

aber über 25 mm CBL, bedingt die höhere Endgröße der Männchen deren Vorherrschen (Tab. 2).

Das Überwiegen von geschlechtsaktiven Männchen in Barberfallen könnte mit deren Kämpfen und Verfolgungsjagden (Bißwunden vorwiegend am Hinterrücken) und nach REICHSTEIN (1956) mit der Suche nach brünstigen Weibchen erklärt werden. So laufen sie vermehrt Gefahr, in Barberfallen zu geraten. Wie sehr das Verhalten aktiver Männchen die zahlenmäßige Relation der Geschlechter in Barberfallen beeinflußt, zeigt auch die Tatsache, daß erst ab einer CB-Länge von 22 mm der männliche Überhang einsetzt (Tab. 1).

Überraschend ist, daß in den Barberfallen von drei Sommern (1981–83), bei sehr verschiedener Dichte und sonst völlig vergleichbaren Verhältnissen, die Männchen zweimal signifikant überwogen. Ferner war unabhängig von der Dichte, die in drei benachbarten Ackergebieten deutlich verschieden war, im Jahre 1981 der Männchenanteil immer signifikant erhöht. Die gegenseitige Elimination reifer Männchen zeigt sich nicht nur im Schlagfallenmaterial (Tab. 2), sondern auch in den Barberfallenfängen von GÖTZ: In der Größenklasse CBL 24–24,9 mm verschärft sich dieser Vorgang genauso (Tab. 1) wie in der Zeit nach der Weizenernte. Diese erfaßt etwa die Hälfte der Ackerfläche und bringt zusammen mit dem nachfolgenden Pflügen den Feldmäusen zusätzlichen Streß (vgl. in Abb. 3 den Unterschied zwischen Juli und August).

Bezüglich des Geschlechterverhältnisses bei der Feldmaus stimmen die Ergebnisse aus Schlagfallenfängen gut mit jenen aus Bauen ausgegrabener Tiere (STEIN 1957) und den Befunden aus Eulengewöllen (BECKER 1954) überein. Wie diese Untersuchung zeigt, ist man trotzdem noch nicht im Stande, sich ein Bild vom realen Geschlechterverhältnis bei *Microtus arvalis* zu machen. Zu berücksichtigen ist auch, daß Barberfallen meist in Form stationärer Fanganlagen eingesetzt werden. DUB (1971) erklärt das Überwiegen von Männchen bis 15 g in seinen Fängen damit, daß diese Tiere in die Lebensräume immigrierten, in denen durch die stationären und beköderten Barberfallen ihre Dichte ständig reduziert wurde.

Danksagung

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Zusammenfassung

In den Jahren 1981 bis 1987 wurden im Marchfeld und in den Donau-Auen östlich von Wien mittels stationärer, unbeköderter Barberfallen (70.615 Falleneinheiten) bzw. Schlagfallen (9.386 Falleneinheiten) 6.547 bzw. 1.055 Feldmäuse, *Microtus arvalis* (Pallas, 1779) gefangen. Die Barberfallen kamen im offenen Ackerland (Sonderstrukturen und Felder) sowie auf Äckern nahe Siedlungen und auf solchen in den Donau-Auen zum Einsatz. Mittels der Schlagfallen wurde an Straßenböschungen des offenen Ackerlandes sowie an verschiedenen extensiv genutzten Wiesen im Augebiet gesammelt. In Schlagfallenausbeuten (Köder Weichkäse oder Margarine) überwogen in Übereinstimmung mit der Literatur die Weibchen, in Barberfallen jedoch von Beginn der Fortpflanzungszeit bis einschließlich Juli, in den meisten Stichproben signifikant, die Männchen. Ab August war in diesen Fängen das Geschlechterverhältnis ausgewogen.

In allen Fällen, in denen ein Geschlecht signifikant überwog, ging dies auf geschlechtsaktive Tiere (Männchen mit Hodengewicht über 130 mg, gravide Weibchen) zurück. Solche Männchen sind lokomotorisch offenbar sehr aktiv, ohne vom Köder besonders angezogen zu werden. Damit erklärt sich ihre hohe Fängigkeit in Barberfallen. Gravide Weibchen haben ebenfalls hohe Mobilität, wofür wahrscheinlich ihr erhöhter Nahrungsbedarf verantwortlich ist. Dementsprechend hat Köder für sie hohe Attraktivität. Diese geschlechtsspezifischen Unterschiede werden offenbar von der Dichte kaum beeinflußt.

Die gegenseitige Elimination geschlechtsreifer Männchen kann auch in den Barberfallenfängen, besonders ab Juli, deutlich erkannt werden. Nach einer Analyse der Anteile verschieden großer Tiere kommt sie jedoch auch schon in früheren Monaten zum Tragen.

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Habitat selection of the Wood mouse (*Apodemus sylvaticus*) in cereal steppes of Central Spain

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Abstract

Studied the distributional patterns of *Apodemus sylvaticus* in an area dominated by cornfield cultivations. Seven habitat variables measured at 44 sampling stations were related to the corresponding summer and winter indexes of mouse abundance by means of multiple regression analysis. In summer, no relationships between habitat features and mouse abundance were obtained. Instead, winter abundance was positively related with shrublands and negatively correlated with grasslands and cultivated fields. This regression model was tested on 68 new sampling stations; predicted and observed values were significatively correlated, thus validating the result. The observed winter distribution patterns are discussed in the light of the thermoregulatory behaviour of mice.

Introduction

The Wood mouse (*Apodemus sylvaticus* L., 1758) is one of the most ubiquitous and abundant small mammals in the Western Palaearctic (Corbet and Southern 1977). Despite its forest origin, it also inhabits cultivated areas, where it can become one of the more abundant small mammal species (Pelikan and Nesvasbova 1979; Angelstam et al. 1987; etc.).

This paper analyses the seasonal distribution of *A. sylvaticus* in Central Iberian cornfields, relating its abundance with some environmental factors and checking the temporal constancy of these relationships.

Study area

The study area is located in the middle of the Iberian Peninsula (41° 13′–41° 18′ N, 3° 44′–3° 48′ W), 1000 m a.s.l. The area belongs to the supramediterranean bioclimatic stage (Ozenda et al. 1979), the climate of which is characterized by hot, dry summers and cold winters (August and January mean temperatures of 20 and 1 °C, respectively, 610 mm annual rainfall; Ministerio de Agricultura 1987). Three main types of substrates are distributed in this open, patchy landscape: 1. shrublands occupying uncultivated areas with thin soil and frequent rocky outcrops, located on the drier slopes and with a vegetation composed of sparse, small bushes (around 20 cm high) of *Thymus zygis, Genista hispanica* and *Astragalus granatensis*; 2. grasslands installed on well-developed soils located in small, wet valleys interspersed with cultivated plots; and 3. cornfields, dedicated mainly to barley, wheat, rye and oat crops. A network of paths and some isolated bushes (*Rosa canina, Crataegus monogyna*) complete the landscape of this man-made steppe (see Tellería et al. 1988 for thorough descriptions of the study area).

Material and methods

An empirical model was established by use of regression analysis (James and McCulloch 1985), which requires obtaining the relative densities of mice in several plots in which habitat features can be measured, so that the abundance of mice (dependent variable) can be finally expressed as a function of some (independent) habitat variables. The model should then be tested by predicting mouse

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abundance in a second selection of plots in which habitat variables had previously been recorded. If predicted and observed values (i.e., actual results of trapping in the second selection) showed similar patterns, the validity of the model proposed would be confirmed (e.g. MORRISON et al. 1987).

In the first round, snap traps baited with cotton wicks steeped in rancid oil were placed in 44 sampling stations. Each sampling station consisted of five capture plots (three snap traps each) located at the corners and in the middle of a 15 m-side square. These capture plots were kept open for two consecutive days and checked daily during December–January, 1984–85, and July–August, 1985 (1320 traps × day each period). In the second round, 68 pitfall traps were set in different locations of the same study area. Each pitfall trap was taken as the equivalent of a first round sampling station and was kept open for 49 days in summer (July–August, 1985) and 35 days in winter (January–February, 1986). Pitfall traps were checked weekly.

To evaluate the habitat features, we defined a 1 ha circular surface area (56 m radius) around each first round sampling station (DUESER and SHUGART 1978) and evaluated by visual estimation (see PRODON 1976; AUGUST 1983) the cover of shrublands, grasslands and cultivated fields; cover of other landscape components such as paths, stones and bushes, that could influence the distribution of the species (HEALING 1980; PARMENTER et al. 1983) was also evaluated. The same variables were considered in the second round, although measured over a smaller area (0.2 ha, 25 m radius around each pitfall trap). Further details on the variables employed can be found in Table 1.

To avoid incidence of zero values, the sampling stations of both rounds were grouped in pairs on the basis of their overall habitat similarity. This provided 22 and 34 analytical units for the first and second rounds, respectively. A stepwise multiple regression equation was used to predict the abundance of Wood mice within the first round (snap traps) data set. The number of captures was included as the dependent variable, and the habitat attributes were used as independent variables. Habitat variables were log-transformed (ZAR 1984). A correlation matrix among all variables allowed us to pair the variables and to remove the ones highly correlated with other easiest to measure and/or with more biological meaning (see YAHNER 1983; MAURER 1986; MORRISON et al. 1987; for similar methodological approaches). Thus, the cover of shrubs lower than 0.5 m and the cover of rocks (Tab. 1) were removed because of their significant correlations with the covers of shrublands ($r = 0.58$, $p < 0.01$) and paths ($r = 0.56$, $p < 0.01$), respectively.

Table 1. **Description of the habitat variables measured**

Variables	Descriptions
Substrates	
1. Grass	Percentage cover of grasslands in a circular surface area (1 ha for first round and 0.2 ha for second), centered around the sampling station.
2. Shrubl	Same as (1) for shrublands.
3. Cult	Same as (1) for cultivated fields.
Structural components	
4. Path	Proportion (in %) in a circular surface area (1 ha for first round and 0.2 ha for second round), centered around the sampling station, ocuppied by paths or country roads.
5. Rock	Same as (4) for stone piles; usually they are extracted as a consequence of farming works.
6. SHR–1	Proportion (in %) in a circular surface area (1 ha for first round and 0.2 for second round), centered around the sampling station, covered with shrubs < 0.5 m in height.
7. SHR–2	Same as (6) for shrubs with height > 0.5 and < 2 m.

Results

During the first and second rounds we caught, respectively, 102 (59 in winter and 43 in summer) and 121 (37 in winter and 84 in summer) mice. The numbers of winter snap-trapped mice were negatively correlated (simple correlation) with the cover of grasslands and positively related with the cover of shrublands. In summer, however, no significant correlation was obtained (Tab. 2). Similar correlation patterns were attained from the

Table 2. **Simple correlations among winter and summer abundance of mice and habitat variables** (see Table 1 for abbreviations)

Mouse abundance	Grass	Shrubl	Cult	Path	SHR-2
First round (n=22)					
Winter	−0.456*	0.540**	−0.310	−0.304	0.233
Summer	−0.106	0.098	0.161	−0.132	0.077
Second round (n=34)					
Winter	−0.382*	0.280	−0.380*	0.163	−0.157
Summer	0.048	0.213	0.099	0.153	0.205

* $p < 0.05$; ** $p < 0.01$.

second round set of data in which mouse distribution was negatively related with the more open substrata (Tab. 2).

No stepwise multiple regression model was obtained with the summer results of the first round, whereas winter mouse abundance was related to grassland and shrubland cover according to the equation Mouse abundance = 2.16 − 1.18 · Grass + 1.54 · Shrubl. (R^2 = 0.32, n = 23, P < 0.01). We checked the validity of this regression model by comparing its predictions with the actual results of the pitfall data set. As both sets of data were obtained by different trapping procedures, we used a simple correlation analysis to test the degree of association of the abundance distributional patterns. The correlation obtained was significant (r = 0.353, n = 34, P < 0.01 one-tailed), thus confirming the similarity of predicted and observed trends of abundance values and the constancy of the effects of the above-mentioned habitat cues (grasslands and shrublands) on the winter distribution of mice in the study area.

Discussion

Despite the well-known interannual variability of density in small mammal populations (e.g., Krebs et al. 1973; Churchfield 1980; Flowerdew 1985; Montgomery 1989a, b), and the different effectiveness of the two trapping methods employed (Tellería et al. 1987), in our study area there was a clear interannual constancy in the winter distributional patterns of Wood mice (e.g., avoidance of pastures and cultivated fields vs. occupation of shrublands).

The relationship between Wood mouse abundance and shrub cover, which has been previously illustrated by several authors (Abramsky 1981; Boitani et al. 1985), can probably be extended to other epigeous small mammal species occasionally entering agricultural, open areas (Rowe and Swinney 1977; Pelikan and Nesvadbova 1979; Ryszkowski 1982; Yahner 1982, 1983). Nevertheless, Wood mice in cereal steppes of Central Spain were clearly seasonal in their response to this habitat feature. In summer, mice seemed to be scattered throughout the landscape, and their abundance was not associated with any habitat variable, whereas in winter they appeared to concentrate in shrublands, avoiding the open substrata (grasslands and cultivated lands; see Tellería et al. 1991). This winter pattern has been related to the thermal homeostasis of the species, which is obliged to build wintering nests in order to prevent lethal heat loss (see West and Dublin 1984). Shrublands were located in dry slopes and offered a high cover of shrubs that provided good nesting opportunities, whereas the wet grasslands and ploughed fields did not seem to facilitate this nesting behaviour. Similar trends have been observed in this and other small mammal species (Kikkawa 1964; Bergstedt 1966; Green 1979; Pelikan and Nesvadbova 1979; Yahner 1982, 1983; Montgomery 1985; Angelstam et al. 1987;

Dickman and Doncaster 1989; Tellería et al. 1991). In winter, these species avoid open, cultivated areas and tend to refuge in closed (bushed or wooded), stable areas (woodlots, shelterbelts, farms, etc.). Our results, showing the importance of shrubland patches as wintering grounds for this species, are consistent with Hansson's (1979) viewpoint that different units in patchy landscapes usually have complementary roles for the survival of vertebrates along the annual cycle.

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Zusammenfassung

Habitatwahl von Waldmäusen (Apodemus sylvaticus) in Getreidesteppen Zentralspaniens

In einer Getreideanbau-Region Zentralspaniens wurden relative Abundanzen von Waldmäusen in drei verschiedenen Habitaten (Getreideäcker, Wiesen, Buschland) in jeweils einer Sommer- und Winterperiode ermittelt. Sieben Habitatvariable wurden an 44 Fangstationen aufgenommen und mittels multipler Regressionsanalyse mit den korrespondierenden Abundanzen verglichen. Für die Sommerfänge ließ sich keine gesicherte Beziehung mit einer der Habitatvariablen feststellen, aber die Winterfänge waren positiv mit Buschland und negativ mit Wiesen und Äckern korreliert. Das Resultat wurde in einer zweiten Runde an 68 neuen Fangstationen überprüft und bestätigt; vorausgesagte und empirisch ermittelte Abundanzwerte waren signifikant korreliert. Der winterliche Rückzug der Waldmäuse von Feldern und Wiesen in Buschland wird im Hinblick auf das thermoregulatorische Verhalten diskutiert.

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Chromosomal multiformity in *Eligmodontia* (Muridae, Sigmodontinae), and verification of the status of *E. morgani*

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Abstract

Studied standard karyotypes of *Eligmodontia puerulus* from Bolivia (6 males, 3 females), and standard and C-banded karyotypes of *Eligmodontia* sp. from Patagonian Argentina (3 males) and Chile (6 males). The former materials amplify the known range for the 2n = 50 cytotype of *E. puerulus.* The latter materials (2n = 32–33) are from localities in close proximity with the type locality of *E. morgani,* and we conclude that these are conspecific. Hence we propose that three species of *Eligmodontia* exist: (1) *E. puerulus* (2n = 50, FN = 48); (2) *E. typus* (2n = 43–44, FN = 44); and (3) *E. morgani* (2n = 32–33, FN = 32). Their distribution is given in Fig. 1.

Introduction

The unstable taxonomic history of the genus *Eligmodontia* Cuvier, 1837 (Muridae, Sigmodontinae) has been reviewed by Tate (1932) and Hershkovitz (1962). *Eligmodontia* has been considered monotypic since Hershkovitz subsumed earlier names under two subspecies, *E. typus* Cuvier, 1837, and *E. typus puerulus* Philippi, 1896. This genus occupies a range of habitats from the Altiplano of Peru and Bolivia to the pampa of Magallanes (Cabrera and Yepes 1940; Mares 1980; Mares et al. 1981; Osgood 1943; Pearson 1951; Pearson et al. 1987), and appears to be the most desert-adapted sigmodontine (Mares 1975, 1977). A recent report (Ortells et al. 1989) documented significant genetic variability in *Eligmodontia* and proposed elevation of the two subspecies of Hershkovitz (1962) to specific status. These species are characterized by 2N = 43–44, FN = 44 (*E. typus*), and 2N = 50, FN = 48 *(E. puerulus).* Ortells et al. (1989) also reported a 2N = 32–33, FN = 32 karyotype from Neuquen Province, Argentina, and suggested that this may represent a third species, but they concluded that data were insufficient to resolve this taxonomic problem. Here we report additional specimens with the 2N = 32, FN = 32 karyotype, extending the distribution of this form to near the type locality of *E. morgani* Allen, 1901, and supporting the specific recognition of *E. morgani.* Additionally, we document the chromosomal complement of *E. puerulus* in Bolivia.

Materials and methods

Chromosomal preparations were obtained from bone marrow following conventional colchicine-hypotonic technique (Baker et al. 1981) as modified by Lee and Elder (1980) for Argentinean and Chilean specimens, and with Velban (Anderson et al. 1987) for Bolivian specimens. C-bands were induced by the barium hydroxide technique (Sumner 1971). Karyotypes were prepared from selected materials, and a minimum of 10 metaphase spreads were counted for each specimen. Nomenclature

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for chromosome morphology and autosomal fundamental number (FN) follow Patton (1967). Chromosomes were arranged and numbered sequentially in order of decreasing size, with single-armed elements preceding biarmed elements.

We analyzed the chromosomes of 18 specimens from five localities in Argentina, Bolivia, and Chile (Fig. 1). These specimens are housed in the Field Museum of Natural History (FMNH), Museum of Southwestern Biology (MSB), and Colección de Mamíferos, Instituto de Ecología y Evolución, Universidad Austral de Chile (IEEUACH). Collection localities are given below and in Fig. 1.



Fig. 1. Map showing locations mentioned in the text. Diploid numbers for *Eligmodontia* spp. are indicated for sites where this information is available. The type locality for *E. morgani* Allen, 1901 is denoted by the star at Arroyo Else

Argentina: Rio Negro Province, Bariloche, 5 km SE Estación Perito Moreno ("Cerro Microondas" of Pearson 1987), 1317 m, ca. 41° S 71° W (3 males, IEEUACH 1738, 1739, 1740).

Bolivia: Oruro Department; 37 km SE Oruro, ca. 3850 m, ca. 18° 21′ S 67° 32′ W (1 male, MSB NK 14518); Estancia Agua Rica, 22 km S Sajama, 3850 m, 18° 20′ S 68° 36′ W (2 males, MSB NK 14526, NK 14544); Rio Barros, 5 km W, 1 km N Pomata Ayte, 3850 m, 18° 19′ S 67° 59′ W (1 male, MSB 14551, 3 females, MSB NK 14552, NK 14554, NK 14560); Potosí Department; 2 km E ENDE camp, Laguna Colorada, 4280 m, 22° 10′ S 67° 47′ W (2 males, MSB NK 14586, NK 14589).

Chile: Lago General Carrera Province, 2 km S Chile Chico, 350 m, 46° 33′ S 70° 56′ W (6 males, FMNH/IEEUACH 133053/3657, 133056/3660, 133059/3663, 133060/3664, 133061/3665, 133063/3667).

Results

The chromosome complement of *Eligmodontia* from all Bolivian sites (2n = 50, FN = 48) is identical to that described by PEARSON and PATTON (1976), and consists of 25 pairs of acrocentric chromosomes (Fig. 2). Four or five of these are large-sized chromosomes, followed by 20 or 21 medium to small pairs. The secondary constrictions reported by PEARSON and PATTON (1976) for chromosome pair 6 were not clearly visible in our samples from Bolivia. The sex chromosomes consist of a medium-sized acrocentric X and a small submetacentric Y.

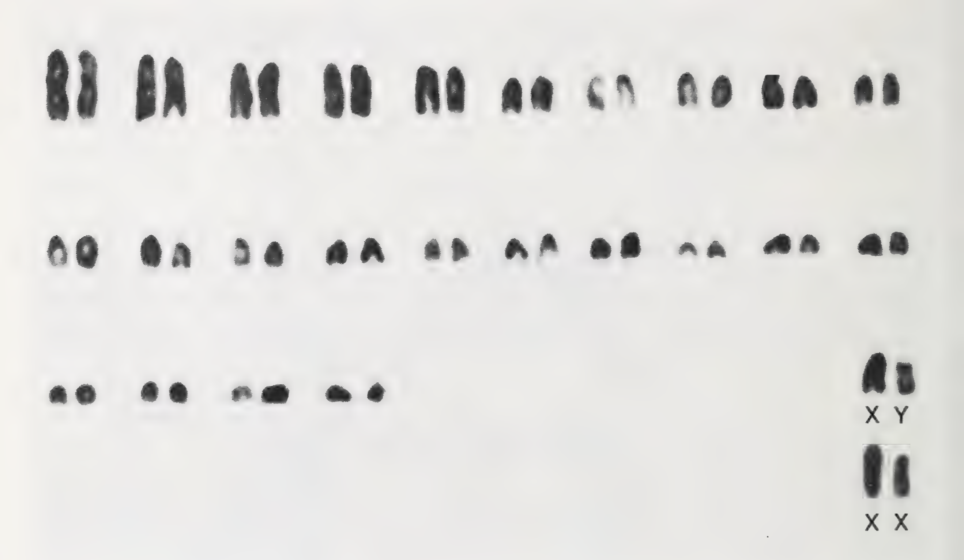


Fig. 2. Standard Giemsa stained karyotype of *Eligmodontia puerulus*. Given is the karyotype for a male from 37 km SW Oruro, and the sex chromosomes of a female from Pomata Ayte

The chromosomal complement of *Eligmodontia* near Chile Chico and at Bariloche (2N = 32, FN = 32) is formed by 14 pairs of acrocentric autosomes (six large; eight medium-sized to small) and one pair of medium-sized metacentric autosomes (Fig. 3). Because we ordered chromosomes by structure and then by size our chromosome pair 15 corresponds to pair number 7 of ORTELLS et al. (1989), and our numbers 7 through 14 correspond to their numbers 8 through 15. The sex chromosomes consist of a medium-sized acrocentric X and a small subtelocentric Y.

The C-banding pattern of the southern form (Fig. 4) is characterized by small amounts of centromeric heterochromatin, except for pairs 11–15, which exhibit conspicuous blocks. Pair 2 has a telomeric block of heterochromatin, which is heteromorphic. The Y chromosome appears totally heterochromatic, while the X does not exhibit a clear C-banding pattern. The lack of a clear pattern in the latter may have resulted from technical problems during preparation.

Discussion

Eligmodontia typus was described from materials collected in "Buenos Aires", Argentina (CUVIER 1837), although the specific locality was unclear. D'ORBIGNY and GERVAIS (1847) later designated the type locality as Corrientes Province. It is doubtful, however, that

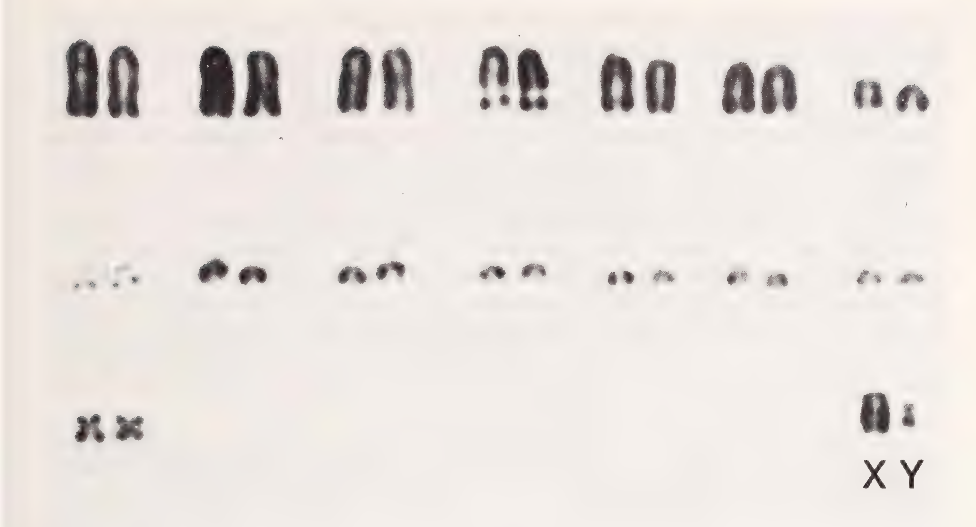


Fig. 3. Standard Giemsa stained karyotope of *Eligmodontia* sp. from Chile Chico, XI Region, Chile, 2n = 32, FN = 32



Fig. 4. C-banded karyotype of *Eligmodontia* sp. from Chile Chico, XI Region, Chile, 2n = 32, FN = 32

Eligmodontia has ever naturally occurred in Corrientes Province (Hershkovitz 1962), and the provenance of the type specimen of *E. typus* remains uncertain (Hershkovitz 1962; see also J. C. Contreras, in Ortells et al. 1989). Philippi (1896) later described *Hesperomys* (= *Eligmodontia*) *puerulus* from San Pedro de Atacama, Antofagasta, Chile.

Although it has generally been agreed that at least two groups exist within the genus, their taxonomic status has remained unresolved. *Eligmodontia puerulus* and *E. typus* were recognized by Osgood (1943, 1947) and Mann (1945), but were relegated to subspecific status by Hershkovitz (1962). Pearson and Patton (1976) accepted Hershkovitz's (1962) arrangement, whereas Reise (1973) and Corbet and Hill (1980) followed Osgood

(1943). Honacki et al. (1982: 410) regarded *Eligmodontia* as monotypic but one reviewer (D. F. Williams) noted that "*puerulus* is probably a separate species". The latter hypothesis was supported by the karyotypic multiformity documented by Ortells et al. (1989), who recommended specific distinction for the two chromosomal forms. These were a 2N = 50, FN = 48 karyotype from Peruvian specimens (Pearson and Patton 1976), and a 2N = 44, FN = 44 karyotype from southern Argentina (Ortells et al. 1989).

Pearson and Patton's (1976) Peruvian specimens were assigned to *E. typus* (Ortells et al. 1989), and implicitly to *E. typus puerulus*. The 2N = 44, FN = 44 cytotype (Ortells et al. 1989) was collected near the type locality of *E. elegans*, which generally has been considered a junior synonym of *E. typus* (references in Ortells et al. 1989). Because of this fact, and the uncertainty of the type locality of *E. typus*, Ortells et al. (1989) applied the name *E. typus* to this karyotype, thereby requiring a reconsideration of the appropriate name for the Peruvian cytotype. The most appropriate available name was *E. puerulus* from northern Chile (Fig. 1; Philippi 1896), acceptance of which effectively elevated *E. typus puerulus* and *E. typus typus* (Hershkovitz 1962) to specific status. Our collections from Bolivia suggest that the 2N = 50, FN = 48 karyotype is continuous with northern Chilean populations of *Eligmodontia*, concurring with Ortells et al.'s (1989) interpretations.

Ortells et al. (1989) also presented a 2N = 32–33, FN = 32 karyotype from the precordilleran steppe of Los Lagos, Neuquen Province, Argentina (Fig. 1), although they considered the systematic and nomenclatural status of this form to be unresolvable with the state of knowledge available to them. Ortells et al. (1989: 137) concluded that the extensive polymorphism and multiformity they encountered indicated that "each of these karyotypes belongs to a different species". However, after reviewing nomenclatural considerations and the geographical arrangement of the southern karyotypic forms, they stated that "it seems that a single species of *Eligmodontia* inhabits the south and the east central Patagonia" (page 138), and they did not assign any specific name to the 2N = 32–33 form collected at Los Lagos.

The present paper documents more thoroughly the chromosomal complement of specimens in the Andean precordillera of southern South America, and demonstrates a consistent pattern in both morphology and banding patterns of these populations, allowing us to extend the results of Ortells et al. (1989). Three chromosomal forms characterize *Eligmodontia* and these are geographically consistent with the proposal that these represent independent lineages with separate evolutionary trajectories. The magnitude of the chromosomal differences between the two southern forms is substantial, indicating that very likely they are reproductively isolated.

This leaves the question of what name to apply to the 2N = 32–33 chromosomal form. Ortells et al. (1989) noted the availability of *E. morgani*, collected at Arroyo Aike, NW Santa Cruz Province, Argentina, and roughly 400 km S Los Lagos, but they expressed concern that their collections at Pampa de Salamanca (2N = 44) were closer to the type locality of *E. morgani* than was their only location for the 2N = 32 karyotype (Los Lagos district, Neuquen Province). Our specimens considerably extend the distribution of the 2N = 32 form southward and suggest that this cytotype may occur throughout western Patagonia. The type locality of *E. morgani* was originally given as "Arroyo Else, Patagonia" (Allen 1901: 409), but it was noted that the description was "based on a large series of specimens collected at or near Cape Fairweather" (Allen 1901: 410), which is roughly 500 km farther south. As noted later by both Osgood (1943) and Hershkovitz (1962), however, the locality on the holotype was "Basaltic Cañons', 50 miles southeast of Lake Buenos Aires, Patagonia" (see Allen 1905: 53, and Hershkovitz 1962: 155). This places the type locality for *E. morgani* within 70 km of our collection sites. In this context, it is interesting to note Osgood's (1943: 199) contention that "specimens from western Rio Negro [Province] seem to indicate that *morgani* may have a northward distribution in

that region". This was accepted by MANN (1978), who referred to *E. typus morgani*, and gave its range as "from Rio Negro to the Strait of Magellan and extreme southern Chile" (1978: 192; translated from Spanish). Finally, although a morphometric investigation has not been undertaken, it should be noted that skulls and skins of specimens from the original collection at Arroyo Else do not visibly differ from those reported here as *E. morgani*.

The specimens reported here help to elucidate the geographic relations of Patagonian cytotypes. Our specimens place the 2N = 32 chromosomal form closer to the type locality of *Eligmodontia morgani* than heretofore documented, and we assume that the distribution of these is continuous. The distribution of this form is western Patagonia in Neuquen, Rio Negro, and Santa Cruz Provinces. Our new specimens alleviate the concerns expressed by ORTELLS et al. (1989) that *Eligmodontia morgani* may be a junior synonym of *typus*, and we recommend specific recognition of *E. morgani*.

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Zusammenfassung

Chromosomale Vielfalt bei Eligmodontia (Muridae, Sigmodontinae) und Bestätigung des Status von E. morgani

Untersucht wurden Standard-Karyotypen von *Eligmodontia puerulus* aus Bolivien (6 Männchen, 3 Weibchen) und Standard- und C-Banden-Karyotypen von *Eligmodontia* sp. aus dem argentinischen (3 Männchen) und dem chilenischen Teil (6 Männchen) Patagoniens. Durch ersteres Material wird die bekannte Verbreitung des 2N = 50 Zytotyps von *E. puerulus* erweitert. Das letztere Material (2N = 32–33) stammt aus nächster Nähe der Typus-Lokalität von *E. morgani*, und wir vermuten, daß es sich um die gleiche Art handelt. Demnach existieren offenbar drei *Eligmodontia*-Arten: 1. *E. puerulus* (2N = 50, FN = 48); 2. *E. typus* (2N = 43–44, FN = 44); und 3. *E. morgani* (2N = 32–33, FN = 32). Die Verbreitung geht aus Abb. 1 hervor.

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The role of sperm morphology in the evolution of Tuco-Tucos, *Ctenomys* (Rodentia, Ctenomyidae): confirmation of results from Bolivian species

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Abstract

Studied sperm morphology and dimensions in five species of caviomorph rodents of the genus *Ctenomys: C. boliviensis, C. frater, C. lewisi, C. opimus* and *C. steinbachi*, collected in Bolivia. All species showed symmetric spermatozoa with paddle-like heads. Dimensions of main sperm components did not vary greatly among species, with mean head and tail lengths of approximately 6.35 and 46 μm, respectively. General morphological characteristics, linear dimensions, and relative sizes of the spermatozoa of these five species were similar to those previously reported for other species of *Ctenomys* that also bear symmetric spermatozoa. The sperm type found in Bolivian *Ctenomys* is in concordance with previous observations which pointed out that symmetric sperm-bearing species inhabit the northern area of the geographic range of the genus, while southern species are characterized by asymmetric spermatozoa. The morphological characteristics of spermatozoa from the Bolivian *Ctenomys*, in conjunction with newly available information, support a previous hypothesis on the role of sperm variants in the reproductive isolation and speciation in this genus.

Introduction

Species of the genus *Ctenomys* Blainville, 1826 (Rodentia, Ctenomyidae) are some of the most specialized and morphologically diverse rodents in Souh America. These fossorial rodents occur in most major habitats south of 10° S latitude (Mares and Ojeda 1982), and since the beginning of the Pleistocene they have undergone an explosive radiation (Reig 1989). They exhibit one of the highest karyotypic diversifications known for mammals, with diploid numbers ranging from 10 to 70 chromosomes (Anderson et al. 1987; Ortells et al. 1990). More than 50 species have been described for the genus (Reig et al. 1990).

Ctenomyids also show many unusual morphological characters, among which the variation in their sperm morphology represents, as far as we know, a unique feature among mammals. Three morphological sperm types are currently recognized for the genus: symmetric, simple-asymmetric, and complex-asymmetric. The nuclear area of simple-asymmetric spermatozoa extends beyond the base of the head forming a "nuclear caudal extension" which runs parallel to the flagellum (see Figure). This peculiar sperm cell was first described for *C. maulinus* from southern Chile (Feito and Gallardo 1976), and later on found in many other species inhabiting the southern area of the geographic range of the genus (Feito and Gallardo 1982; Vitullo et al. 1988). The complex-asymmetric spermatozoon shows two nuclear caudal extensions, which has so far been described for a single species, *C. yolandae* (Vitullo and Roldán 1986a). Symmetric spermatozoa lack the nuclear caudal extension (see Figure) and characterize the species inhabiting the northern area of the geographic range of the genus. The association between sperm morphology and geographic distribution in *Ctenomys* was first noticed by Feito and

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Gallardo (1982) and confirmed in further studies (Altuna et al. 1985; Vitullo et al. 1988).

The clear-cut distribution of two groups of species bearing a given sperm type, and the low interspecific variability in morphological patterns and dimensions of sperm cells within each group have led to the supposition that sperm variants appeared at an early stage in evolution of *Ctenomys* and played a major role in the first steps of speciation by promoting the separation of two lineages, which underwent, independently, an explosive speciation related to high rates of chromosomal repatterning (Vitullo et al. 1988).

In this study, we report the analysis of spermatozoa from five species of *Ctenomys* collected in Bolivia, and discuss these results in the light of newly available information on other research fields, which support the hypothesis previously advanced on the role of sperm morphology in the evolution of *Ctenomys*.

Materials and methods

Morphological characteristics of spermatozoa were studied in five species of *Ctenomys* distributed in Bolivia. Species and trapping localities were as follows: *C. boliviensis* (N = 5), Department of Santa Cruz; *C. frater* (N = 2), Tarija, 8 km E Rancho Tambo; *C. lewisi* (N = 2), Tarija, 1 km E Iscayachi; *C. opimus*, Potosí, Laguna Colorado (N = 1), and Oruro, 7 km S, 3 km E Cruce Ventilla (N = 1), and Oruro, Huancaroma (N = 3); and *C. steinbachi* (N = 5), Department of Santa Cruz. Voucher specimens were preserved at the Museum of Southwestern Biology, University of New Mexico, Albuquerque, New Mexico, and the American Museum of Natural History, New York, USA.

Spermatozoa were prepared as previously described (Vitullo et al. 1988). In brief, cauda epididimydes fixed in glutaraldehyde were minced with sharp scissors. Sperm suspensions were smeared onto cleaned slides, air-dried, rinsed in tap water, and stained with Giemsa according to Watson (1975).

Sperm cells were examined under bright field microscopy and measured with an ocular micrometer at a magnification of 630×. The following sperm components were measured and expressed as mean values: head length, head width, midpiece length, tail length and total length (head plus flagellum).

Results and discussion

The spermatozoa of *C. boliviensis, C. frater, C. lewisi, C. opimus* and *C. steinbachi* were found to belong to the symmetric type, lacking the nuclear caudal extension. The cells showed paddle-like, caudally truncated heads with tails inserting centrally into the base of the head (Fig. 1a). Alterations to this pattern were not found among individuals or between species. The sperm type found in Bolivian species agrees with previous observations that the species bearing symmetric spermatozoa are distributed in the northern geographic range of the genus (Feito and Gallardo 1982; Vitullo et al. 1988).

Sperm dimensions (Tab. 1) did not vary among the five species studied, with mean head and tail lengths of approximately 6.35 and 46.0 μm, respectively. Linear dimensions of main sperm components were found to be very close to those previously reported for other species of *Ctenomys* with the same sperm type (Vitullo et al. 1988). Of the five species studied, previous information on sperm morphology has only been reported for *C. opimus* from Chile (Feito and Gallardo 1982). Differences were not found in sperm dimensions between Chilean and Bolivian *C. opimus*.

Although sperm morphotypes are strikingly different (see Figure), and symmetric spermatozoa are shorter than the asymmetric forms, a very low interspecific morphometric variability has been shown to exist within each group, and relative sizes of head, midpiece, and tail were found to be invariable in the three sperm types (Vitullo et al. 1988). Results on Bolivian *Ctenomys* confirm these observations. Sperm dimensions do not show interspecific variability (Tab. 1), and relative sizes of the main sperm components are within the range of other species bearing the symmetric sperm type (Tab. 2).



(a) Symmetric spermatozoa from *C. boliviensis*. The same sperm type was found in *C. frater, C. lewisi, C. opimus* and *C. steinbachi*. Currently recognized sperm types in *Ctenomys:* (b) symmetric, (c) simple-asymmetric, (d) complex-asymmetric. Arrowheads show the nuclear caudal extension(s) characterizing asymmetric spermatozoa. (Bar = 10 μm)

No association between a given sperm type and low or high chromosomal numbers has been previously found (VITULLO et al. 1988). Diploid numbers in Bolivian *Ctenomys* range from 2n = 10 in *C. steinbachi* to 2n = 56 in *C. lewisii* (ANDERSON et al. 1987; COOK et al. 1990, confirming the lack of association between chromosomal variation and sperm types. In addition, alterations either in morphology or linear dimensions of symmetric spermatozoa among individuals of *C. boliviensis* (a chromosomally polymorphic species, 2n = 36–46, cf. ANDERSON et al. 1987) were not found.

Table 1. **Sperm dimensions (μm) in Bolivian *Ctenomys***

Species	Head length	Head width	Midpiece length	Tail length	Total length
C. boliviensis	6.35 ± 0.51	3.21 ± 0.47	6.18 ± 0.53	46.04 ± 1.04	52.39 ± 1.18
C. frater	6.35 ± 0.57	3.12 ± 0.49	6.12 ± 0.53	45.91 ± 1.26	52.24 ± 1.44
C. lewisi	6.34 ± 0.56	3.16 ± 0.51	6.26 ± 0.56	46.17 ± 1.27	52.46 ± 1.34
C. opimus	6.34 ± 0.51	3.20 ± 0.48	6.10 ± 0.54	46.30 ± 1.02	52.65 ± 1.24
C. steinbachi	6.33 ± 0.52	2.85 ± 0.65	5.97 ± 0.56	46.03 ± 1.26	52.32 ± 1.24

Due to the clear-cut distribution of species of *Ctenomys* bearing symmetric and asymmetric spermatozoa, the interspecific constancy of both morphology and dimensions of the sperm types, and the lack of association of sperm types with chromosomal characteristics, VITULLO et al. (1988) proposed the following scenario for the evolution of

Table 2. **Mean relative sizes of sperm components in Bolivian *Ctenomys***

Species	Percentage of mean total length Head	Midpiece	Tail
C. boliviensis	12.12	11.80	87.88
C. frater	12.15	11.71	87.88
C. lewisi	12.08	11.94	88.02
C. opimus	12.04	11.58	87.94
C. steinbachi	12.10	11.41	87.97
Symmetric Sperm[1]	12.31 (12.02–12.81)	11.50 (11.41–11.76)	87.47 (86.89–87.98)

[1] Mean and range of relative size for symmetric sperm type taken from Vitullo et al. (1988).

Ctenomys: 1. sperm variants appeared at an early stage in evolution, 2. the early appearance of sperm variants played a major role in reproductive isolation during early speciation prior to geographical dispersal, and 3. chromosomal events leading to high speciation in the genus occurred after the original separation of two groups of species as a consequence of the reproductive isolation promoted by the early appearance of sperm variants. Symmetric spermatozoa were considered to represent the ancestral or plesiomorphic condition for *Ctenomys* because they are very close to those of other Caviomorpha, and to the eutherian ancestral type (Vitullo and Roldán 1986b; Vitullo et al. 1988; Roldán et al. 1991). On the other hand, the longer asymmetric sperm was considered to be the apomorphic condition. The major predictions of our previous hypothesis are supported by the present results as discussed above, and by newly available information form other research fields.

Recently, Rossi et al. (1990) have isolated a highly repetitive DNA sequence of about 370 kbp from *C. porteousi*, a species bearing simple asymmetric spermatozoa. Heterologous hybridization of this sequence with DNA from many other species of *Ctenomys* has shown that the sequence is widespread in the genus. Nevertheless, hybridization patterns are species-specific and, significantly, *C. opimus* displays a weak hybridization signal only under permissive conditions (Rossi et al. 1990). The low intensity of the signal found in *C. opimus* is quite similar to that of other Octodontidae, suggesting that the expansion of the sequence occurred in species with asymmetric spermatozoa after the divergence of this phylogenetic lineage from species with symmetric sperm cells. These results support our hypothesis that a symmetric spermatozoon represents the ancestral condition for the genus. In addition, a detailed analysis of the trends in evolution of sperm shape and size in rodents pointed out that simple symmetric spermatozoa represent the ancestral type not only for Caviomorpha but for Muridae and Cricetidae, and eutherian mammals in general (Roldán et al. 1991).

Rossi et al. (1990) suggested that at least two genomic lines may have evolved in *Ctenomys* with regard to the patterns and the degree of amplification of the highly repetitive DNA sequence. While not mentioned by the authors these lines are characterized by a different sperm type, further supporting the idea of an early appearance of sperm morphotypes in the evolution of *Ctenomys* (Vitullo et al. 1988).

Based on chromosome affinities, it was recently shown that the different species of *Ctenomys* may be grouped in five well-defined clusters which probably represent evolutionary units (Ortells 1990). Every cluster is characterized by a sperm morphotype, with minor exceptions (Ortells 1990; Reig pers. comm.), reinforcing the idea that explosive chromosomal evolution took place after the original separation of two groups of species as a consequence of reproductive isolation promoted by the early appearance of sperm variants (Vitullo et al. 1988).

Finally, it is important to note that the hypothesis involving sperm morphotypes in the evolution of *Ctenomys* represents a novelty for speciation in rodents. The proposal that sperm variants triggered a mechanism of strong reproductive isolation which determined the separation of two lineages, implies as a corollary the necessity of some kind of gametic incompatibility. Significantly, it was argued that a main function of the nuclear caudal extension is to increase the contact area between sperm and egg at fertilization (Feito and Barros 1982). Studies on in vitro and in vivo cross fertilizations may shed light on the cellular and molecular basis of such a mechanism of gametic incompatibility.

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Zusammenfassung

Die Rolle von Spermienmorphologie in der Evolution der Kammratten, Ctenomys (Rodentia, Ctenomyidae)

Untersucht wurde die Spermienmorphologie von 5 caviomorphen Rodentia-Arten der Gattung *Ctenomys* aus Bolivien: *C. boliviensis, C. frater, C. lewisi, C. opimus* and *C. steinbachi.* Alle Arten verfügen über relativ einheitlich gebaute symmetrische Spermien mit paddelförmigen Köpfen. Für morphometrische Daten ergaben sich bei durchschnittlicher Länge der Kopf- und Schwanzregion von 6,35 bzw. 46 μm nur geringe Unterschiede im zwischenartlichen Vergleich. In morphologischen Kennzeichen und Maßen ähneln die Spermien dieser fünf Arten ferner anderen *Ctenomys*-Vertretern mit symmetrischen Spermien. Damit wird erneut bestätigt, daß Kammrattenarten aus dem nördlichen Teil der Gesamtverbreitung symmetrisch gebaute Spermien haben. Für Arten aus dem südlichen Teil sind hingegen asymmetrische Spermien kennzeichnend. In Übereinstimmung mit anderen Befunden werden diese Unterschiede aus evolutionsbiologischer Sicht diskutiert.

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On eye lens weights and other age criteria of the Brown hare (*Lepus europaeus* Pallas, 1778)

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Abstract

Described the eye lens growth of 42 age-known brown hares (*Lepus europaeus*) by regression models including confidence limits. In addition, lens weights of 369 free-living specimens from the wild were compared with three other indicators of age: "Stroh-sign" i.e. epiphyseal protrusion of the ulna, flexibility of processus lacrimalis and degree of ossification of skull sutures. Due to the slow growth rate and the high individual variability of lens weights in adults estimation of years of age is not possible, but segregating juveniles and adults can be achieved by determination of eye lens weights. Furthermore, within juvenile hares eye lens weights serve for estimation of the date of birth. The "Stroh-sign" appears to be only a crude indicator for separating juveniles from adults. Both the processus lacrimalis and the state of ossification of skull sutures are of no value for a reliable discrimination of juvenile and adult hares.

Introduction

Among the various methods proposed for ageing brown hares (Stroh 1931; Kleymann and Schneider 1974; Frylestam and v. Schantz 1977; Habermehl 1985) the determination of dry eye lens weights has been reported to be sensible enough for the discrimination of juveniles (i.e. youngs of the year or individuals not older than 9–10 months of age) and adult hares (Caboń-Raczyńska and Raczyński 1972; Pepin 1974). In adults years of age can be assessed with sufficient accuracy by counting the annual periosteal adhesion lines of the mandible (Frylestam and v. Schantz 1977; Pascal and Kovacs 1983). In juveniles periods of births have been estimated roughly by Pegel (1986) using the eye lens growth curve presented by Pepin (1974), which was constructed according to an equation based on a non-linear regression of eye lens weight on real age of hares. However, the appropriate solution for ageing by using eye lens weights requires a regression of real age on eye lens weights, thereby minimizing variation of age (comp. e.g. Myers and Gilbert 1968 for wild rabbits, *Oryctolagus cuniculus*; Dapson 1980). Moreover, Pepin's growth curve does not include confidence intervals as recommended by Dapson (1980). The reference curve for ageing brown hares by means of eye lens weights published by Broekhuizen and Maaskamp (1979) has been fitted by eye.

The main objectives of this paper are 1. to give a new non-linear regression model for the growth of eye lenses based on age-known brown hare individuals, 2. to present both the curves and the confidence limits of the regression of age on eye lens weight and 3. to evaluate the reliability of various other methods for ageing brown hares by comparison with ages as indicated by dry eye lens weights, respectively.

Material and methods

From a total of 411 hares presently used 359 individuals were shot by hunters in the course of regular hunts in autumn 1988 in different parts of Austria covering a wide range of environmental conditions

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(comp. Hartl et al. 1989). Further 10 specimens were obtained during an extra hunt in summer 1989 in the region of "Marchfeld" (approx. 30 km east of Vienna). In addition, a sample of 42 individuals was taken from the brown hare breed at the Forschungsinstitut für Wildtierkunde und Ökologie (Vet. Med. University) in Vienna. The latter specimens were ear-tagged animals maintained in cages and fed commercial pellets ad libitum; their exact days of birth were known.

All animals were sexed by inspection of internal reproductive organs. Palpation of the lateral ulnar knob close to the carpal joint (epiphyseal protrusion – "Stroh's sign" of juvenile individuals; comp. Stroh 1931) has been carried out on one forelimb and repeated on the other one whenever the first check gave a negative result.

In 167 heads of hares obtained from hunters the praeorbital lateral processus lacrimalis had been proved for flexibility by palpation through the pelt before eyeballs were removed. The processus lacrimalis is supposed to remain flexible in juveniles until sufficient ossification has occurred; thus it may serve as a criterion to discriminate juveniles and adults (Habermehl 1985). In 172 hares stemming from the various hunting areas both eye balls were removed within 30 minutes to 6 hours after death. The eyeballs of the 42 cage-reared individuals were removed immediately after death. There was no predetermined schedule for sacrifying cage-reared hares for the purpose of the present study. Other individuals (n = 197) were either stored cool at 4 °C for variable time (up to 10 days) or frozen at −20 °C for 1 to 2 months before eye balls were removed. Fixation of total eye balls was performed in 10 % formalin for 2 months. Desiccation of the lenses of 344 individuals was carried out in a normal air pressure oven ("Heraeus type TU HO") at 100 °C for 24 hours solely. The lenses of 55 hares were weighed after drying for 24 hours and 48 hours, respectively. Weighing of a further sample of 58 lenses from 35 hares was done after 24, 48, 72, 96, 120 und 161 hours of desiccation. Weighing was performed on an analytical balance to the nearest 0.1 mg. The weights of 396 lenses were determined immediately after drying for 24 hours and once again after having been left for cooling off at normal room temperature for 15–30 minutes. In 269 specimens age category was determined according to the ossification of skull sutures following the scheme provided by Caboń-Raczyńska (1964) and additionally after a slightly modyfied scale. For all statistical tests significance was considered at the 0.05 % level of probability if not mentioned otherwise.

Results

The drying process and intraindividual variation

The course of reduction of lens weights during 161 hours of desiccation is shown in Figure 1. The average increase of dry weights of lenses permitted to cool off for 15–30 minutes

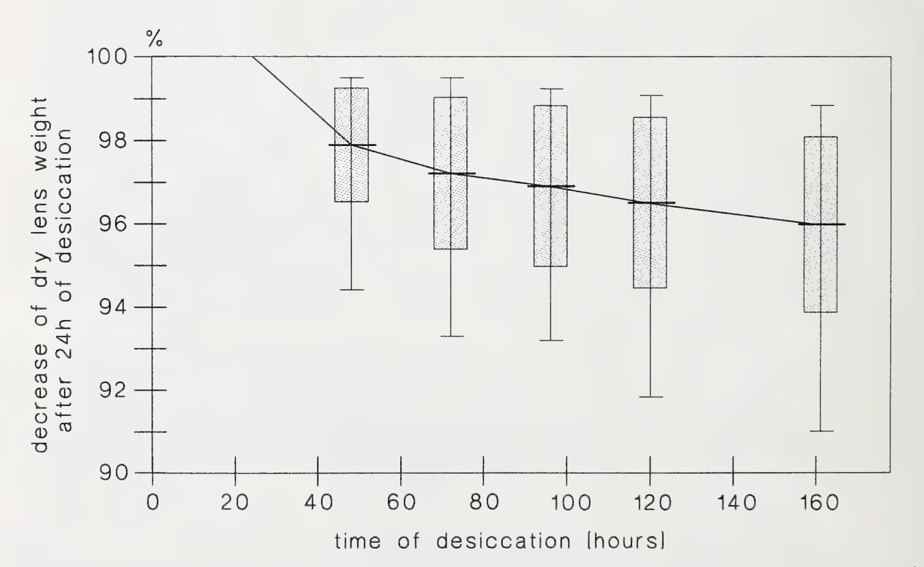


Fig. 1. Reduction of eye lens weights of Brown hares (n = 58 lenses from 35 specimens). Lens weights are given in % of the respective weights after 24 h of drying. Mean, standard deviation, minimum and maximum is given for weights gained after 48, 72, 96, 120 and 161 h, respectively

after removing from the oven was $\bar{x} = 0.3$ mg (s.d. = 0.31, min. = −0.6, max. = 1.6, n = 396 lenses after drying for 24 hours). The intraindividual differences (right vs. left) of dry lens weights were found to be $\bar{x} = 7.45$ mg (s.d. = 6.6, min. = 0.0, max. = 23.0, n = 42 lenses dryed for 24 hours), $\bar{x} = 5.1$ mg (s.d. = 4.3, min. = 0.0, max. = 16.2, n = 42 lenses dryed for 48 hours) and $\bar{x} = 3.4$ mg (s.d. = 2.9, min. = 0.0, max. = 12.7, n = 42 lenses dryed for 161 hours). Weights of lighter lenses of pairs averaged $\bar{x} = 1.22$ % (s.d. = 1.0, max. = 3.9, min. = 0.0) less than the heavier ones, respectively, after drying for 161 hours. In 82.6 % of lens pairs that lens which had been the heavier one of both after 24 hours of drying remained to be the heavier one of both after 24 hours of drying remained to be the heavier one throughout the total period of desiccation (161 hours). Between the dry lens weights (DLW) gained after 24 hours (DLW_{24}) and 48 hours (DLW_{48}) of desiccation a very strong correlation ($R^2 = 0.9999$, n = 26) was found; the linear regression of DLW_{48} on DLW_{24} ($DLW_{48} = 0.975 \times DLW_{24}$) including the 95 % confidence intervals is shown in Figure 2.

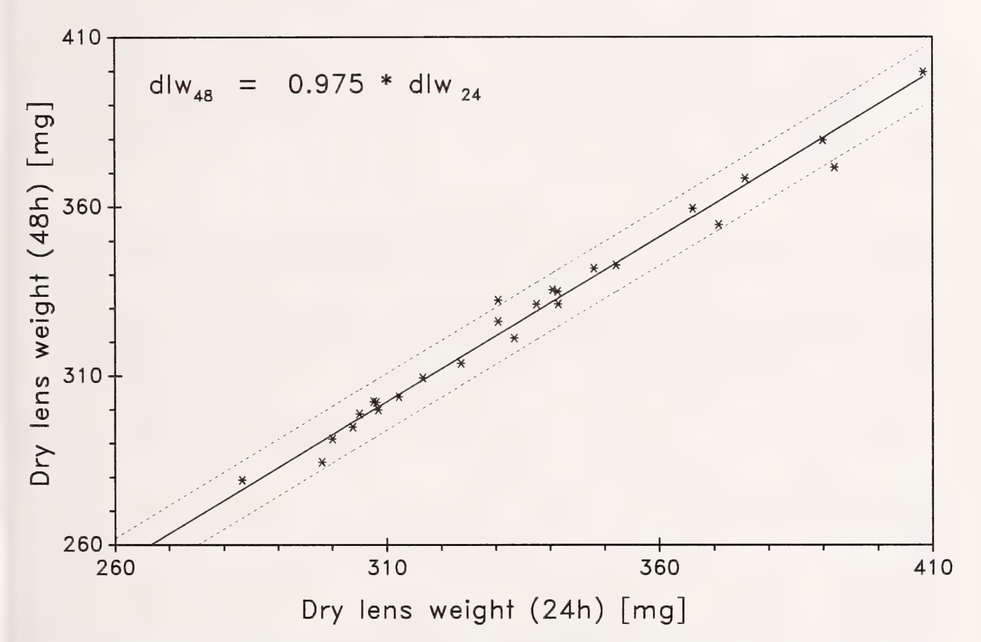


Fig. 2. Relationship of lens weights gained after 24 and 48 h of drying, respectively. Dotted lines indicate 95 % confidence range

Accordingly further analyses concerning dry lens weights were performed on the basis of DLW_{24}. Furthermore, any individual dry lens weight was calculated as the arithmetic mean of both lenses, with few exceptions in cases of damages of one eye.

Eye lens growth and the ageing curve

In the literature (e.g. Myers and Gilbert 1968; Connolly et al. 1969) normally transformations of $x = \frac{a}{Age + b}$ and $y = \log(DLW)$ are found to be applied to make their relations linear. The parameters a and b are evaluated by testing several values and using the best. Trying a non-linear approach by optimizing these parameters using a gradient method (comp. Hartley 1961) no convergence to an optimal solution was found

presently. All results proved inferior to using logarithmic transformations for age and DLW_{24}. Retransforming the results of the linear regression yields the representations:

DLW_{24} (mg) = 29.76 × age (days)$^{0.3721}$, $R^2 = 0.9582$ for all age-known specimens (n = 42),

DLW_{24} (mg) = 23.11 × age$^{0.4326}$, $R^2 = 0.9932$ and

age (days) = 0.0007646 × DLW_{24} (mg)$^{2.2958}$, $R^2 = 0.9932$ for individuals younger than 454 days of age (n = 20).

Growth of eye lenses of 42 pen-raised brown hare specimens is characterized by means of the regression curve in Figure 3. There was no indication of different growth of lenses in respect of the sex (comp. PEPIN 1974). According to the confidence limits in Figure 3 interindividual variation in eye lens weights increased especially from the second year of life onward, after main growth has been already accomplished. In Figure 4 the relationship of real age and DLW_{24} calculated separately for the first 453 days of life (20 individuals), to reduce the 95 % confidence interval during the main growth period, is presented. To enable direct estimation of age by using DLW_{24}, the equation and the curve including the 95 % confidence limits of the regression calculation of age on DLW_{24} based on the same 20 individuals is presented in Figure 5. In addition, estimated ages and respective lower and upper confidence limits are given in Table 1 for selected DLW_{24} (as recommended by DAPSON 1980).

Eye lens weights and other age indicators

In Figure 6 the frequency distribution of DLW_{24} of hares collected during the autumnal hunting season and the respective percentage of individuals exhibiting a "Stroh-sign" within each DLW_{24}-class are presented. In both sexes hares without a "Stroh-sign" occurred first in the DLW_{24}-class 185–195 mg (see Fig. 6), indicating an age of 123 (97–155 conf. range) days (comp. Fig. 5). Within the DLW_{24}-class 275–285 mg (317 days of age, 237–425 conf. range; comp. Fig. 5) no hare showed a "Stroh-sign"; however, few animals

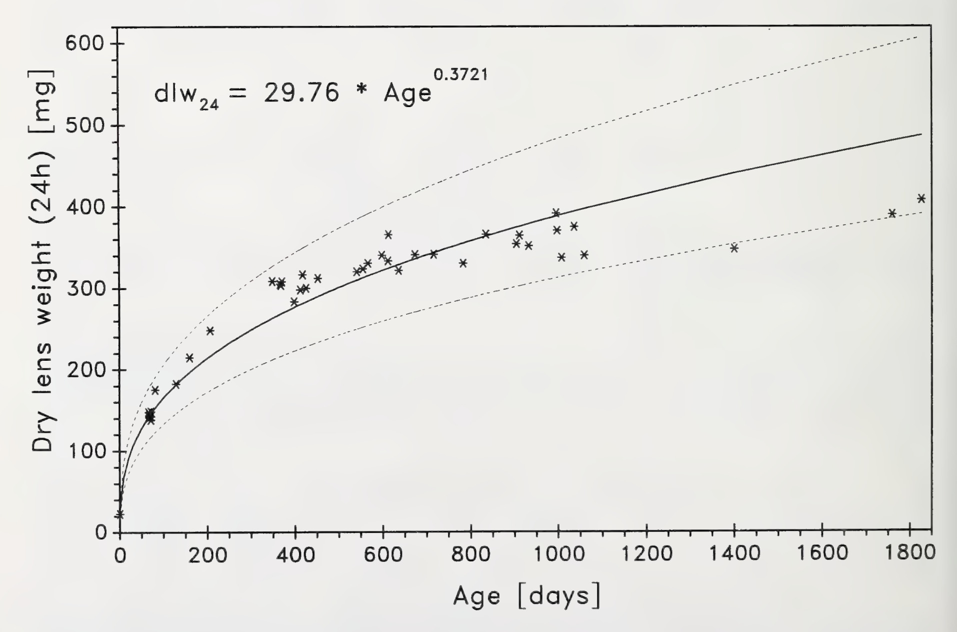


Fig. 3. Growth curve of age-known pen-reared Brown hares (n = 42 specimens). Dotted lines indicate 95 % confidence range

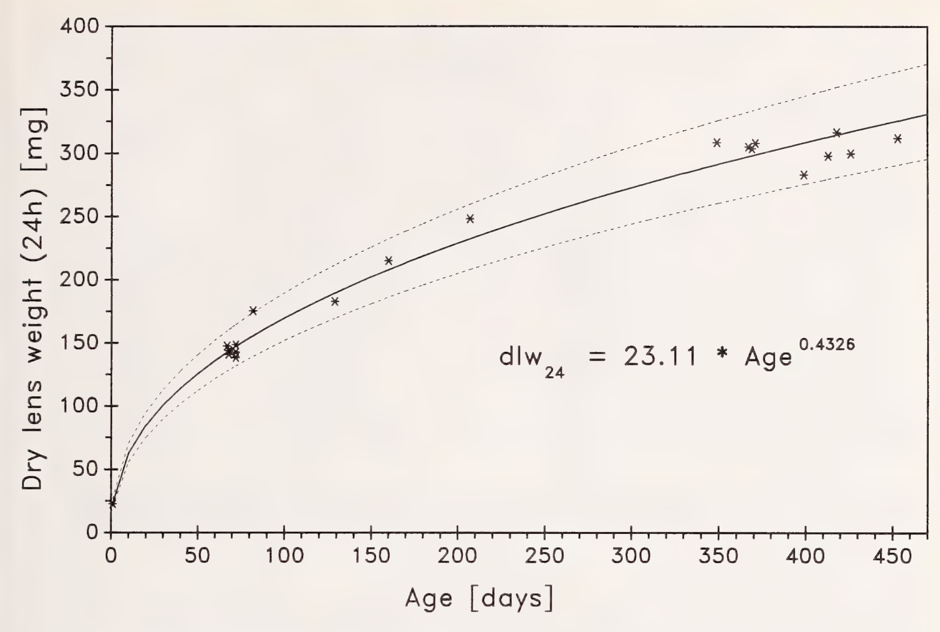


Fig. 4. Growth curve of age-known pen-reared Brown hares (n = 20) younger than 454 days of age. Dotted lines indicate 95 % confidence range

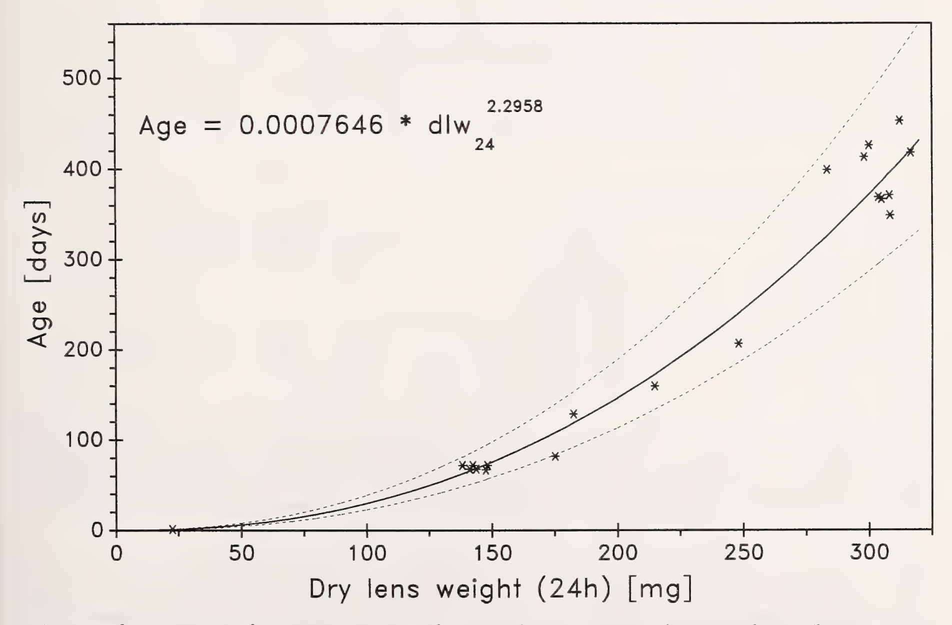


Fig. 5. Reference curve for age-estimation of Brown hares younger than 454 days. The regression calculation is based on the same individuals (n = 20) as in fig. 4. Dotted lines indicate 95 % confidence range

Table 1. **Estimated ages and 95 % confidence intervals of Brown hares based on the regression equation**

Lens weight (mg)	Estim. age (days)	95 % conficence interval (days)	(months)
25	1.5	1.1–1.4	0
50	6.1	5.1–7.2	<0.3
75	15.4	12.7–18.7	0.4–0.6
100	29.9	24.3–36.7	0.8–1.2
125	49.8	40.2–61.8	1.3–2.1
150	75.7	60.6–94.7	2.0–3.2
175	107.9	85.7–135.8	2.9–4.5
200	146.6	115.8–185.7	3.9–6.2
225	192.1	150.9–244.6	5.0–8.5
250	244.7	191.3–313.0	6.4–10.4
275	304.6	237.1–391.2	7.9–13.0
300	371.9	288.4–479.6	9.6–16.0
325	446.9	345.3–578.4	11.5–19.3

$y = 0.0007646 \times x^{2.2958}$ for selected values of dry lens weights (24 h of desiccation). Regression equation and variance were based on dry lens weights of 20 hares 453 days old or less (comp. Fig. 5).

with a "Stroh-sign" were detected in some higher DLW_{24}-classes. This reveals, that the disappearence of the "Stroh-sign" may already occur within the fourth month of life and it might be still present at least in some specimens older than one year. There was no tendency of the "Stroh-sign" to disappear earlier in one of the sexes (Kruskal-Wallis-test on DLW_{24} in male and female "Stroh-positive" hares). Few individuals occurred in DLW_{24}-class 275–285 mg (see Fig. 6) indicating an age of 10.6 (7.9–14.2) months (comp. Fig. 5); this corresponds to the cessation of reproduction during the period October–December in central European hare populations, consequently leading to a low number of individuals 8–14 months of age in the autumnal sample (comp. Caboń-Raczyńska and Raczyński 1972; Broekhuizen and Maaskamp 1979; Pegel 1986). Thus, within the

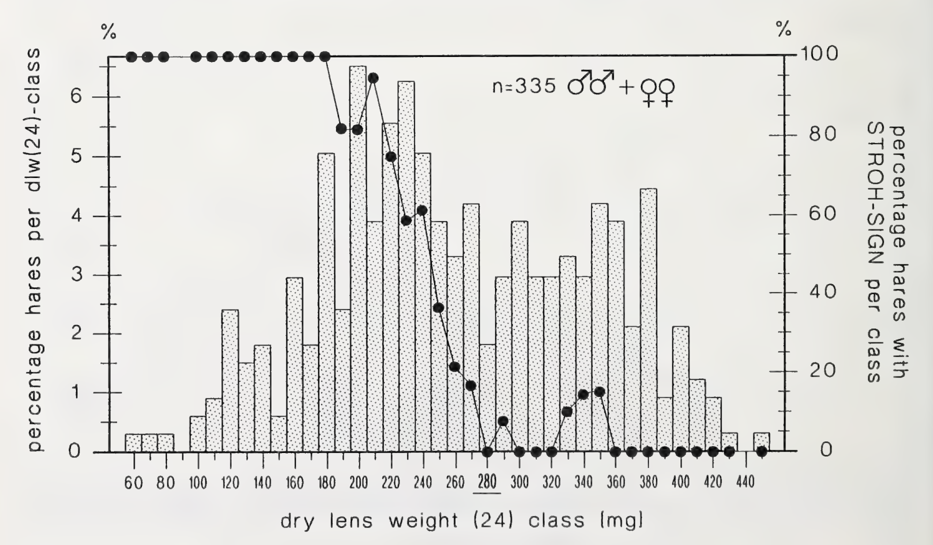


Fig. 6. Frequency distribution of eye lens weights of 335 wild living Brown hares sampled during the autumnal hunting season 1988 (histogram, left ordinate). Percentage occurrence of specimens with a "Stroh-sign" in each lens weight class (full circles, right ordinate)

present autumnal sample all specimens with $DLW_{24} < 275$ mg are considered as juveniles (youngs of the year). When discriminating juveniles and adults using the "Stroh-sign" and comparing the results with respective DLW_{24} values 100 % agreement was achieved in hares sampled in October; however, accordance was lower in specimens from November (84.1 %) and the first half of December (79.2 %).

Palpable flexibility of the processus lacrimalis in juvenile hares ($DLW_{24} < 275$ mg, n = 90) was given in only 55.6 %. Moreover, DLW_{24} did not differ significantly between juveniles (palpable "Stroh-sign") with a flexible processus lacrimalis on the one hand and with an ossified one on the other. In adults 10 % of the processus were flexible.

Ages of skulls were categorized into four consecutive classes according to the progress of the ossification of sutures (sutura sagittalis, sutura frontalis, sutura parietotemporalis and sutura coronaria) as discribed by Caboń-Raczyńska (1964). However, it appeared, that ossification was generally somewhat reduced in the present material as compared to the hares investigated by Caboń-Raczyńska (1964): especially sut. parietotemporalis and sut. coronaria hardly showed an ossification. Therefore, presently the oldest age class (number 4 in Caboń-Raczyńska 1964) was characterized by (almost) complete ossification of sut. sagittalis and sut. frontalis but not necessarily by ossification of sut. parietotemporalis and sut. coronaria. The relationship of skull age classes and the respective DLW_{24} values is presented in Figure 7. Despite of extended zones of overlap significant differences in

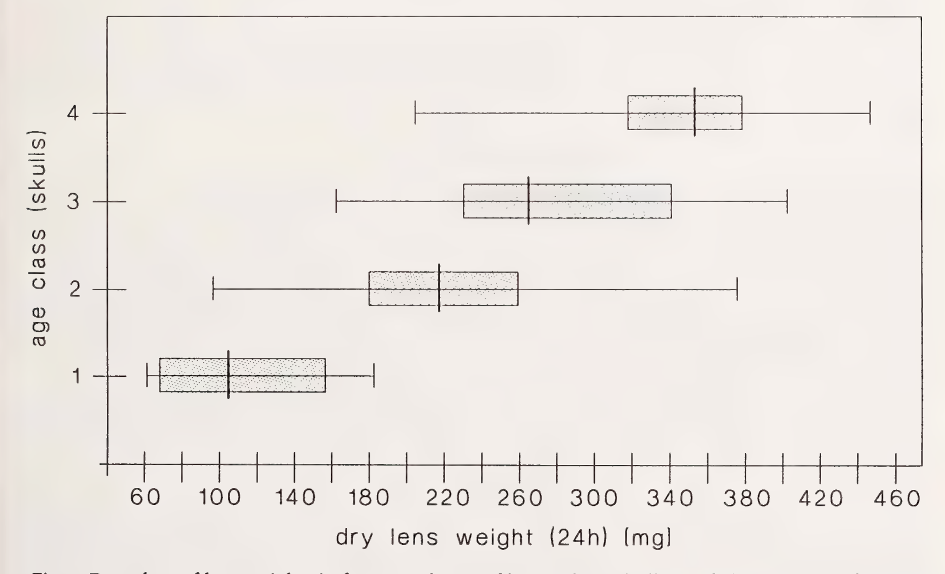


Fig. 7. Box plots of lens weights in four age classes of brown hare skulls (n of class 1 = 6, n of class 2 = 153, n of class 3 = 50, n of class 4 = 60). Age classes of skulls were determined according to the slightly modified scheme of ossification of sutures provided by Caboń-Raczyńska (1964); comp. also section "results". Medians, range of second and third quarters, minima and maxima are given

DLW_{24} were found between the four age categories of the skulls (Kruskal-Wallis-test of DLW_{24} in the four groups, $p < 0.0001$, d.f. = 3) confirming the progress of ossification with increasing age. No tendency of sex-specific differences concerning ossification of skulls was detected (Kruskal-Wallis-tests on DLW_{24} values between the sexes for each of the four skull age groups). Within a sample of age-known brown hares from the breed (n = 27) skull age class four (indicating the highest step of ossification) was reached first at an age of 418 days. However, among specimens at least 418 days old (n = 22), only 31.8 %

could be attributed to age class 4, 31.8 % to age class 3 and 36.4 % to age class 2. The maximal age of an individual in age class 2 (start of ossification of sut. sagittalis and sut. frontalis) was 962 days!

Discussion

Eye lens weights of hares are reported to depend to a certain degree on the specific procedures of desiccation as temperature, duration, use of hygroscopic substances and application of reduced air pressure (Andersen and Jensen 1972; Caboń-Raczyńska and Raczyński 1972; Pepin 1974; Broekhuizen and Maaskamp 1979). Freezing and decomposition prior to fixation reduced lens weights in cottontails (*Sylvilagus floridanus*) (Pelton 1970) and in raccoons (*Procyon lotor*) (Montgomery 1963) but not in domestic sheep (Longhurst 1964). According to Montgomery (1963) lens weights of raccoons were not affected by decomposition when lenses were left within the eye balls for up the three days at room temperature. Apart from such influences, present findings concerning intraindividual variability suggest occurrence of fluctuating asymmetry (comp. e.g. Soulé 1967) in lens masses, possibly determined by varying potentials for maintaining developmental homeostasis (Zakharov 1981).

Most of water evaporation of lenses was already accomplished after 24 hours of desiccation at 100 °C (Fig. 1). Thus, mean values of DLW_{24} were used for the construction of a lens growth curve extending from one to 1800 days of age (Fig. 3). The regression curve in Figure 3 does not appear to represent the best fitting line and the rate of lens growth in adult specimens is most likely to be slower than indicated by the respective regression formula; however, there was no simple relationship feasable to convey the saturation of DLW_{24} at a level of approx. 350 mg (comp. Fig. 3). Using more parameters to explain the relationship of DLW_{24} and age would raise the degree of uncertainty about these parameters and consequently increase the confidence region. Because of the reduced growth rate and the considerable individual variation of DLW_{24} in adult specimens determination of DLW_{24} is an inappropriate technic for assessing years of age in adult brown hares. Nevertheless, the rapid growth of eye lenses and the comparatively narrow confidence interval of DLW_{24} within the first year of life (Fig. 4) enable estimating the months of age in juveniles (Fig. 5 and Tab. 1). Thereby, the approximate month of birth of a juvenile hare can be determined by dating back from the date of hunt.

However, it is emphasized, that the present growth curves have been constructed by using captive animals which may have somewhat heavier lens weights than free-living hares (comp. e.g. Rongstad 1966 for cottontail rabbits, *Sylvilagus floridanus*). Furthermore, differences in the rate of lens growth between various wild populations may also occur (comp. Connolly 1969 for the black-tailed jack rabbit, *Lepus californicus*). The low frequency of DLW_{24} ranging from 275 to 285 mg (Fig. 6), indicating an age of 10.6 (7.9–14.2) months (comp. Fig. 5), is in good correspondence with the reproductive pause of central European hare populations (October–December), consequently leading to few individuals 9–14 months of age in the autumnal sample. Accordingly hares with $DLW_{24} < 275$ mg were presently determined as youngs of the year. Similar DLW limits for juveniles were found by Caboń-Raczyńska and Raczyński (1972), Pepin (1974), Broekhuizen and Maaskamp (1979) and Pegel (1986).

When using the "Stroh-sign", which occasionally may already be absent in animals 4 or 5 months of age (Fig. 6), to segregate juveniles and adults in the present autumnal hare sample, the chance of incorrect ageing as compared with the respective DLW_{24} increased from 0 % in October to approx. 20 % in November and the first half of December. This is a consequence of higher portions of older juveniles in the samples from November/ December (comp. e.g. Caboń-Raczyńska and Raczyński 1972). Since one or the other juvenile individual may have a $DLW_{24} > 275$ mg (comp. Tab. 1) and consequently would

not have been grouped as a juvenile for the purpose of this comparison, the percentages of wrong ageing in November and December as given above should even be somewhat higher. In this study, occasionally adult hares ($DLW_{24} > 275$ mg) were found to have a "Stroh-sign" (Fig. 6); they are considered, however, as having been categorized as „Stroh-positive" by mistake. When segregating juveniles and adults within a given sample by using the "Stroh-method" the percentage of wrong determinations depends both on the time of the year the animals have been sampled and the particular age structure of the juveniles within the sample (comp. also CABOŃ-RACZYŃSKA and RACZYŃSKI 1972). In conclusion, the "Stroh-method" is merely a crude way to discriminate juvenile and adult brown hares. If applied in analyses for hunting management it must be taken into account, that the percentage of juveniles per sample estimated by the "Stroh-method" represents only a minimal value and that no general constant for correction can be given.

Ossification of the skull sutures starts already within the first year of life and increases generally with age, but the high individual variability (Fig. 7) does not allow age estimations by using the scheme of CABOŃ-RACZYŃSKA (1964). A reliable discrimination of juveniles and adults is impossible by this method. Also, the flexibility of the processus lacrimalis did not prove useful for segregation of juvenile and adult hares.

Acknowledgements

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Zusammenfassung

Über Augenlinsengewichte und andere Altersmerkmale beim Feldhasen (Lepus europaeus Pallas, 1778)

Bei insgesamt 411 Feldhasen aus Österreich wurden die Trockengewichte der Augenlinsen, die Verknöcherung der Ellen-Epiphyse („Stroh'sches Zeichen"), des Processus lacrimalis und der Verknöcherungsgrad der Schädelnähte ermittelt. Anhand der Linsengewichte von 42 Tieren mit bekanntem Alter aus einer Feldhasenzucht wurden Regressionsmodelle des Linsenwachstums sowie eine Regression zur Altersschätzung von Hasen erstellt. Während die Linsengewichte eine Trennung von Jung- und Althasen und bei Junghasen außerdem eine Einteilung in einzelne Geburtsperioden ermöglichen, ist bei adulten Tieren wegen des verlangsamten und individuell stark variierenden Linsenwachstums keine Altersgliederung nach Jahren möglich. Das „Stroh'sche Zeichen" ist nur als grober Indikator, der Processus lacrimalis und die Schädelverknöcherung sind überhaupt nicht zur Trennung von Jung- und Althasen geeignet.

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WISSENSCHAFTLICHE KURZMITTEILUNGEN

Karyotype of the East European hedgehog, *Erinaceus concolor*, from Jordan

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Acceptance of Ms. 23. 05. 1991

The European hedgehog, *Erinaceus europaeus*, was recognized as a single, highly polymorphic species with several subspecies (Ellerman and Morrison-Scott 1951). Introduction of new karyological techniques revealed differences between these populations in heterochromatin distribution (Gropp 1969; Gropp et al. 1969) that were otherwise unnoticed by conventional techniques (Kral 1967). After the introduction of the simplified C-banding technique, Mandahl (1978) demonstrated species-specific differences between the Eastern and Western European forms of the hedgehog. Multivariate analyses also document differences in skull morphology with few intermediate backcross hybrids seen in Poland and the former Silesia (Holz 1978). However, as pointed out by the latter author, the earliest available names for these two species are: 1. *Erinaceus europaeus* described by Linnaeus (1758, Syst. Nat., 10th ed., p. 52) from Wamlingbo, South Gothland Island, Sweden, and 2. *Erinaceus concolor* Martin (1918, Proc. Zool. Soc. Lond., p. 103) described from near Trebizond, Turkey.

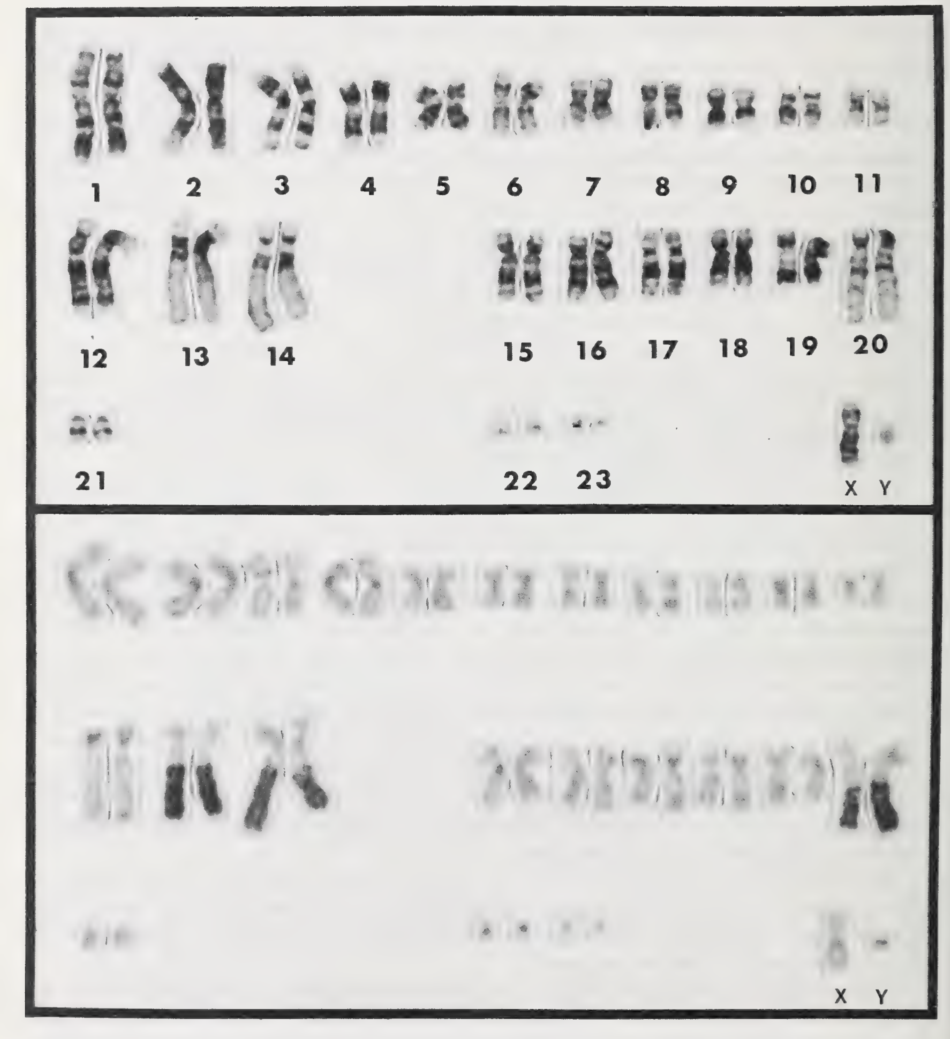
The European hedgehog *(Erinaceus)* is represented by a single species in the Near East. It can be distinguished from the other hedgehogs by its large size (head and body length ranges from 200–260 mm in adults with skull length over 55 mm), relatively short ears, and lack of a dorsal bare patch on the nape (Harrison 1964). Thomas (1918) reported a specimen from "near Jerusalem" which he described as a separate subspecies: *E. roumanicus sacer.* Based on geographical and morphological considerations Harrison (1964) and Atallah (1977) allocated the Eastern Mediterranean forms to the synonymy of *E. europaeus concolor.* As pointed out by Holz (1978), although the differences between *E. europeaus* and *E. concolor* are significant in populations studied from Europe, there is potentially a third form (perhaps *E. roumanicus*) found in Romania and Bulgaria. I report on the G- and C-banded karyotypes of *Erinaceus* from Jordan and comment on the status of this group in the Near East. This study is intended to demonstrate that the Jordanian *Erinaceus* is indeed *E. concolor* and to compare the karyotype of the Jordanian hedgehog with that of the East European hedgehog.

Ear and lung biopsies were taken in the field from a male captured in Jbeihah, Jordan. The establishment of cell culture, harvest, slide preparation and banding techniques follow those of Baker and Qumsiyeh (1988). Five G-banded and five C-banded metaphases were photographed and karyotypes prepared.

G-banded and C-banded karyotypes of *Erinaceus* from Jordan arranged and numbered as suggested by Mandahl (1978) show complete homology for all chromosomes when comparing the G-band pattern to those specimens karyotyped from eastern Europe. The large blocks of heterochromatin in my specimen are also situated on chromosome numbers

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13, 14 and 20 as can be seen from comparison of the G- and C-banded karyotypes (Fig.). Other chromosomes do not show any heterochromatic blocks. In all these karyotypic characteristics, the Jordanian specimen clearly resembles *Erinaceus concolor* (the Eastern European hedgehog) rather than *E. europaeus* of western Europe. It is indeed remarkable that no significant difference could be detected between the karyotypes of the specimen from Jordan and some karyotypes of *E. concolor* described from such distant countries as Greece (Giagia and Ondrias 1980) and Poland (Mandahl 1978). A recent study by Grafodatski et al. (1986) on *E. concolor* reveals that these C-band positive heterochromatic regions consist of highly repetitive DNA. It is tempting to speculate that there is a functional significance to the karyotypic uniformity of heterochromatin distribution in *Erinaceus concolor* or that heterochromatic additions played a role in speciation in European hedgehogs (Gropp et al. 1969).



G-banded (upper) and C-banded (lower) karyotypes of *Erinaceus concolor* from Jordan arranged and numbered as suggested by Mandahl (1978)

Thanks are due to Mr. MAHER ABU JAAFAR and the Royal Society for the Conservation of Nature (RSCN) for the permit to study mammals in Jordan. I also thank RASMI JARRAR who collected the specimen of *Erinaceus* studied here and Dr. DUANE A. SCHLITTER for reading the manuscript.

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A comparison of the effects of a moss diet and a varied diet on the growth of juvenile Wood lemmings, *Myopus schisticolor* (Lilljeb.)

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Receipt of Ms. 15. 04. 1991
Acceptance of Ms. 21. 06. 1991

Animals that include mosses in their diet tend to live in cold environments. PRINS (1981) argued that moss could be an important component in the diet of these animals because it contains arachidonic acid, which is an anti-frost agent. The consumption of mosses may be particularly important for animals such as the wood lemming, *Myopus schisticolor,* which reproduce during winter (MYSTERUD et al. 1972; KRATOCHVIL et al. 1979; BONDRUP-NIELSEN et al. 1991).

Very few animals consume mosses; however, the wood lemming has an extreme preference for them. In 518 wood lemmings caught during the summer, over 90 % of the stomach contents consisted of mosses (BONDRUP-NIELSEN 1991), and in a food-preference experiment wood lemmings showed a distinct preference for mosses. Wood lemmings consume mosses mainly during the winter (KALELA et al. 1963). BONDRUP-NIELSEN (1991), however, found that wood lemmings also eat a small amount of grass and dwarf-shrubs. Here, we tested the importance of plant species other than mosses for the growth of juvenile wood lemmings.

The study took place in Varaldskogen, SE Norway in the summer of 1988. Sixteen juvenile (12–18 g) wood lemmings were captured between 1 June and 15 July. Seven animals were kept alone in small cages (30 × 30 × 20 cm), and 9 animals in groups of 2 to 4 individuals in large cages (70 × 70 × 20 cm). Eight animals received only mosses, 70–100 % of which were *Dicranum* spp., which constitutes a major part of the wood lemming diet (BONDRUP-NIELSEN 1991). The remaining 8 animals received a varied diet consisting of mosses, grass, blueberry bushes and rolled oats. The lemmings were weighed upon capture, and again at the end of a test period, which lasted from 4 to 8 days. There was no relationship between the time spent in the test and the criteria of diet (Mann-Whitney $U = 24.5$, $p = .41$). The growth rate (g/day) during the test period was calculated for each individual. During the test, there was always excess food available, and the moss was kept moist by spraying.

To test if there was any difference in the growth rate we performed a two-way analysis of covariance (ANCOVA), where the growth rate was the dependent variable, and weight at capture the covariate. The experimental treatments (factors) that could influence growth were the food regime (mosses or varied diet), and the social environment of the animal (alone or with other individuals together in the cage).

The ANCOVA showed a significant effect of weight at capture (Table), but when this effect of the covariate was removed the diet had an even more significant effect on juvenile growth rates ($p = .0031$). The mean growth rate was higher for animals receiving the varied diet. Whether the animals were kept alone or together in a cage had no significant effect on the growth rate.

This study therefore suggests that the inclusion of plant material other than mosses in the diet of wood lemmings enhances their growth, although BONDRUP-NIELSEN (unpubl.

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Growth rate ($\overline{X}$ ± S.E.) and sample sizes of the different treatment groups tested

Statistics presented from ANCOVA with weight at capture as the covariate

	g/day (± S.E.)	n	F-ratio	p
Covariate				
Weight at capture			5.305	0.042
Diet				
Only mosses	0.06 (± 0.07)	8	14.181	0.003
Varied	0.51 (± 0.13)	8		
Social environment				
Alone	0.25 (± 0.09)	7	3.114	0.105
Together	0.31 (± 0.15)	9		

data) found that wood lemmings survive and grow to maturity on a diet consisting solely of mosses.

Recent studies of rodents on low-quality diets have revealed the existence of special mechanisms in the intestinal system and feeding behaviour of several species that assure a maximum absorption of nutrients (Batzli 1989; Björnhaug 1989; Erkinaro 1989). Nevertheless, our study suggests that low quality food is not necessarily optimal, not even for species that are partially adapted to such low quality food as mosses.

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First records of *Microtus (Pitymys) felteni* in Albania

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Acceptance of Ms. 21. 5. 1991

A series of small mammals endemic to Albania comprises a portion of the collection of mammals at the National Museum (Natural History) in Prague. This material was collected by the members of the Institute of Parasitology of the Czechoslovakian Academy of Sciences in 1958. The collection consists of various species of rodents and shrews as well as two specimens of voles of the subgenus *Pitymys,* formerly determined by collectors as *Pitymys savii* (see Daniel 1960). However, a recent reevaluation of these specimens left no doubt that they belong to *Microtus (Pitymys) felteni* (Malec and Storch, 1963). The validity of this determination is supported mainly by the pattern of enamel of the third upper molar, which is identical to that described by Niethammer (1982).

Two specimens of this species were trapped on May 10, 1958 in the pass of Llogora (Mali i-Cikës Mts., Central Albania) at an altitude of approximately 1050 m above sea level. The skins and damaged skulls are preserved in our collections.

The body and some measurements of the skull are as follows (in mm): NM P6V-40132 (female ad.)/NM P6V-40133 (male juvenile): head and body 91/84; tail 28/25; hindfoot 15.5/14.5; ear 8/7; condylobasal length -/19.5; diastema length 6.6/5.8; zygomatic width -/12.2; least interorbital width 4.1/3.9; alveolar length of upper tooth row 5.7/4.9; alveolar length of lower tooth row 5.3/4.8.

According to the present knowledge on the general distribution of *Microtus (Pitymys) felteni* (Niethammer 1982; Brunet-Lecomte 1990) we can conclude that these specimens represent the first records of this species in the territory of Albania at present.

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BEKANNTMACHUNG

Protokoll über die Mitgliederversammlung der Deutschen Gesellschaft für Säugetierkunde e.V. am 23. September 1991 im Hörsaal des Zoologischen Instituts der Universität Hamburg

Der 1. Vorsitzende, Herr KULZER, eröffnet die Versammlung um 17.00 Uhr.

1. Die Tagesordnung wird angenommen mit der Maßgabe, daß über den Brief der Herren HUTTERER und BOYE vor Erörterung des Punktes 7) diskutiert wird.
2. Herr SCHMIDT verliest den Bericht über das abgelaufene Geschäftsjahr 1990. Im Berichtsjahr erschien der 55. Band der „Zeitschrift für Säugetierkunde" in 6 Heften mit 432 Seiten. Zusätzlich wurde allen Mitgliedern das Sonderheft mit den Kurzfassungen der Vorträge und Posterbeiträgen der Tagung in Osnabrück zugesandt.
   Auf Einladung der Herren SCHRÖPFER und EVERTS fand die 64. Hauptversammlung der Gesellschaft vom 23.–27. September 1990 in Osnabrück statt. Themenschwerpunkte waren „Ökologie", „Ontogenie" und „Ernährung und Verdauung". Erneut wurden herausragende Poster durch Buchprämien ausgezeichnet, welche die Verlagsbuchhandlung Paul Parey dankenswerterweise gestiftet hatte.
   Die Konstanz der Mitgliederzahl beruht auf dem Zuwachs von Mitgliedern aus den neuen Bundesländern. Von insgesamt 609 Mitgliedern stammen 34 von dort.
   Durch den Tod verlor die Gesellschaft folgende Mitglieder:
   Prof. Dr. J. BOESSNECK, München,
   Prof. Dr. H. DATHE, Berlin,
   Prof. Dr. G. KÜHNE, Berlin,
   Prof. Dr. E. VON LEHMANN, Bonn,
   Prof. Dr. H. SÄGESSER, Bern
   Dr. V. WENDLAND, Wiesbaden.
3. Frau KÜHNRICH erläutert den von ihr vorgelegten ausführlichen Jahresabschluß.
4. Die Kassenprüfer BOHLKEN und SCHLIEMANN haben keinen Anlaß zu Beanstandungen gefunden.
5. Die Anträge zur Entlastung des Schatzmeisters und des Vorstandes werden bei Enthaltung des Vorstandes und einer Gegenstimme angenommen.
6. Als Kassenprüfer für das Geschäftsjahr 1991 werden die Herren BOHLKEN und SCHLIEMANN wiedergewählt.
7. Der 1. Vorsitzende verliest die „Gedanken zu einer Reform der DGS", welche die Herren HUTTERER und BOYE am 10. September 1991 dem Vorstand übermittelt hatten. In der lebhaften Diskussion, die sich daran anschließt, wird die Bildung einer Kommission, die neue Gedanken zur Förderung der DGS erarbeiten soll, einstimmig befürwortet. Per Akklamation werden als Kommissionsmitglieder bestimmt die Herren BOYE, FRÄDRICH, HUTTERER, MAIER, SCHLIEMANN, SCHRÖPFER und STUBBE. Herr HUTTERER wird beauftragt, die Vorschläge der Kommission zu sammeln, damit sie im August allen Mitgliedern zur Kenntnis gebracht werden können.
8. Für den neuen Vorstand, der vom 1.1. 1992 bis 31.12. 1996 amtieren soll, schlägt Herr KULZER im Namen des alten Vorstandes Frau KÜHNRICH und die Herren SCHMIDT, STUBBE, FIEDLER, HUTTERER, ERKERT und FRÄDRICH zur Wahl vor. Schriftlich, einzeln und geheim werden von den Mitgliedern gewählt als:

1. Vorsitzender:	Herr SCHMIDT
2. Vorsitzender:	Frau FEDDERSEN-PETERSEN
3. Vorsitzender:	Herr FIEDLER
Beisitzer:	Herr HUTTERER

Geschäftsführer: Herr ERKERT
Schatzmeister: Frau KÜHNRICH
Schriftführer: Herr FRÄDRICH

Die Gewählten nehmen die Wahl an.

9. Der Vorstand sieht keine Veranlassung zur Veränderung des Mitgliedsbeitrages für 1992. Er beträgt DM 95,– für Vollmitglieder, DM 60,– für Studierende, DM 10,– für Ehepartner und DM 65,– für Mitglieder aus dem Osten Deutschlands. Die Versammlung schließt sich dieser Auffassung mit einer Gegenstimme an.
10. Die Mitglieder nehmen die Einladung von Herrn RIETSCHEL an, die 66. Hauptversammlung vom 20.–24. September 1992 in Karlsruhe abzuhalten. Als Schwerpunktthemen werden „Chiroptera“, „Paläontologie“ und „Sozialverhalten der Säugetiere“ gewählt. Die Einladung von Herrn MAIER, 1993 in Tübingen zu tagen, wird durch Akklamation angenommen.
11. Herr KULZER gibt bekannt, daß der Fritz-Frank-Förderpreis auch in diesem Jahr nicht vergeben werden kann.
12. Der Vorstand gibt bekannt, daß er die Herren FRICK und STRAUSS zu Ehrenmitgliedern benannt hat.
13. Unter dem Beifall des Auditoriums dankt Herr HUTTERER Herrn KULZER für seine langjährige erfolgreiche Tätigkeit als 1. Vorsitzender der Gesellschaft.

Die Sitzung endet um 19.45 Uhr.

Prof. Dr. E. KULZER, 1. Vorsitzender — Prof. Dr. U. SCHMIDT, Geschäftsführer — Dr. H. FRÄDRICH, Schriftführer

WALTON, D. W.; RICHARDSON, B. J.: **Fauna of Australia.** Vol. 1B: Mammalia. Canberra: Australian Government Publishing Service 1989. 1227 pp., num. figs and tables. 79.95 $. ISBN 0-644-05484-0

Recently, the Australian government published a multivolume set on the fauna of this continent. This volume deals with mammalian species, exclusively and is a modern, comprehensive compilation to characterize mammals of Australia and their biological significance. The volume is edited by D. W. WALTON and B. J. RICHARDSON, however, the various chapters represent contributions of altogether 57 experts, the majority from Australian scientific institutions.

The book consists of chapters 14–64. Starting with a more general characterization of the class Mammalia the following two chapters are attributed to the monotremes. In the three consecutive chapters marsupials as a group are introduced in a general overview dealing with morphology, physiology, natural history, biogeography and phylogeny. The same is done for the eutherians in three later chapters. The remaining chapters cover the special biology of the diverse forms. The taxonomic unit described is the Family. These descriptions are predominately done according to an overall pattern: definition and general description, history of discovery, morphology and physiology, natural history, life history, ecology, behaviour, biogeography, phylogeny, collection and preservation, classification, literature. The last two chapters deal with collection and preservation of mammals and contain an illustrated key at the generic level. Altogether the Families Tachyglossidae and Ornithorhynchidae as well as 14 marsupial Families including their diversity of species are characterized. The eutherian mammals considered are of the orders Chiroptera (7 Families), Rodentia (2), Lagomorpha (1), Cetacea (6), Carnivora (4), Sirenia (1), Perissodactyla (1) and Artiodactyla (4). Thus, native extant and lately extinct as well as introduced wild forms, feralized domestic stock and natural invaders are described. The text is concisely and informatively written and older as well as recent literature of different linguistic origin is cited. There are also several tables and numerous instructive and in some cases impressive figures. Most chapters on eutherian mammals are clearly shorter than those on the native forms.

This volume can be recommended to mammalogists as a highly welcome and very instructive synopsis on the mammals of this continent written by well-informed scientists. D. KRUSKA, Kiel

MOSIMANN, W.; KOHLER, T. (Hrsg.): **Zytologie, Histologie und mikroskopische Anatomie der Haussäugetiere.** Berlin, Hamburg: Paul Parey 1990. 338 S., 290 Abb., 13 Tab. Geb. DM 148,–. ISBN 3-489-51 616-8

Hier ist ein Werk zu besprechen, welches die Bezeichnung „Lehrbuch“ zu vollem Recht trägt. Obwohl insgesamt 14 Autoren an der Abfassung des Buches beteiligt waren, ist ein gelungener, einheitlich gestalteter, sorgfältig – dabei aber nicht überladen – illustrierter Band entstanden, der jedem empfohlen werden kann, der zytologisches, histologisches und mikroskopisch-anatomisches Grundwissen erwerben möchte. Die Autoren bieten klare Begriffsdefinitionen und benutzen eine eindeutige Sprache. Durch die Typograpie wird der Text stark gegliedert, so daß Lektüre und Studium erleichtert werden.

Nach einem Kapitel, welches eine Einführung in die Zytologie bietet, wird in vier Kapiteln die Histologie von Epithelien, Binde- und Stützgeweben sowie von Muskel- und Nervengewebe dargestellt. Auf mehr als 200 S. wird in insgesamt 15 Kapiteln die mikroskopische Anatomie von Organsystemen besprochen. Klar gestaltete Tabellen bieten in übersichtlicher und kondensierter Form wichtige histologische und mikroskopisch-anatomische Daten. Im Vergleich zu dem 1960 im gleichen Verlag erschienenen „Lehrbuch der Histologie und vergleichenden mikroskopischen Anatomie der Haustiere“ von Krölling und Grau fällt auf, daß in dem hier vorgestellten Band in einem eigenen Kapitel (etwa 30 S.) die mikroskopische Anatomie des Immunsystems und der Organe der Abwehr behandelt wird. Es verwundert allerdings, daß sich dieses moderne Lehrbuch, im Gegensatz zur „vorigen Generation“, in Titel und Inhalt auf Haussäugetiere beschränkt.

Der Leser, welcher an weiterführender Literatur interessiert ist, findet fünf Seiten mit entsprechenden Angaben. Aus anderen Werken übernommene Abbildungen sind klar gekennzeichnet und ein sechsseitiges Sachverzeichnis erschließt den Inhalt und erleichtert das Nachschlagen.

Der Referent ist davon überzeugt, daß das vorliegende Lehrbuch nicht nur für Studierende der Tiermedizin, sondern für alle an der Mikrostruktur des Körpers der Säugetiere interessierte Leser von großem Nutzen sein wird. P. LANGER, Gießen

Dyban, A. P., Baranow, W. S.: **Die Zytogenetik der Säugetier-Embryogenese.** Experimentelle Studien zu den Irrwegen und zur Auslese während der Verteilung des Genoms. Pareys Studientexte 64. Berlin und Hamburg: Verlag Paul Parey 1989. Aus dem Russischen von Petra Pawel, deutsche Bearbeitung W. Sachsse. 276 S., 8 Abb., 28 Tafeln, 36 Tab. kart. DM 38,–. ISBN 3-489-51016-X

Der Titel ist insofern irreführend, als es hier nicht um die Steuerung der Ontogenese, sondern um die Beziehung zwischen lichtoptisch erkennbaren Veränderungen im Karyotyp und damit korrelierte Abweichungen in der Embryonalentwicklung geht. Seit die Chromosomen der Säugetiere zuverlässig gezählt und vor allem aufgrund von Bandenfärbungen identifiziert werden können, sind hier eine Menge neuer Erkenntnisse, vor allem am Menschen und an Labormäusen, gewonnen worden. Bei der Labormaus führte die Entdeckung von Populationen mit zentrischen Fusionen normalerweise telozentrischer Chromosomen zu der Möglichkeit, Trisomien und Monosomien jedes einzelnen Chromosoms zu gewinnen und zu analysieren. Das vorliegende Buch, dessen Original in 2. Auflage 1988 in russischer Sprache erschienen ist, faßt die Befunde derartiger Untersuchungen zusammen und stützt sich dabei auf ein umfangreiches, 25 S. umfassendes Literaturverzeichnis. Die Autoren, die selbst zahlreiche experimentelle Beiträge geleistet haben, behandeln das Thema kritisch und können vielfach scheinbar widersprüchliche Befunde aufgrund ihrer Kenntnis der methodischen Schwierigkeiten einheitlich deuten. Für den Taxonomen interessant sind z. B. die Angaben über Non-Disjunction bei Nachkommen von Eltern mit unterschiedlichen Chromosomenzahlen und die Häufigkeit und Folgen der daraus resultierenden Monosomien oder Trisomien. Obwohl die Kapitel folgerichtig angeordnet, und in sich logisch gegliedert und durch Zusammenfassungen sowie tabellarische Übersichten ergänzt sind, ist das Buch aus zwei Gründen schwer verständlich. Einmal wird viel vorausgesetzt, was dem Nicht-Zytogenetiker Schwierigkeiten bereitet, wie die Terminologie der Hausmaus-Chromosomen. Zum anderen scheint die deutsche Übersetzung mangelhaft. So ist auf S. 66 von provisorischen Organen, vom Augennerv und von Hirnkammern die Rede, auf S. 91 von einzelligen Embryonen und auf S. 90 von einer Morula-Blastozyste. Der Goldhamster ist hier stets ein „Syrischer Hamster". In der Unterschrift zu Tafel X gibt es eine „Verzögerung der Herzkammern" (gemeint ist offenbar eine Verzögerung ihrer Bildung), S. 122 einen „Dosis-Gen-Effekt".

Fazit: Eine fundierte Zusammenstellung über Chromosomenanomalien bei den Säugetieren, ihre mögliche Entstehung und Auswirkung, als Studientext aber leider allenfalls für sehr fortgeschrittene Studenten zu empfehlen.

J. Niethammer, Bonn

Dinse, H.: **Informationsverarbeitung im visuellen System der Katze.** Stuttgart, New York: Thieme 1989. 204 S., 8 Tab., 66 Abb., 9 Bildtafeln, DM 44,–. ISBN 3-13-729 501-7

Diejenigen Funktionen des Neocortex, die eine besondere Herausforderung an die Forschung darstellen, sind Assoziations- und Integrationsleistungen, kurz: die Informationsaufarbeitung. Dinse hat das mit (elektro)physiologischen und psychophysischen Methoden bei der Katze untersucht. Ableitungen von Neuronen der primären Sehrinde (Area 17) und weiteren visuell beeinflußten Areae (Areae 18, 19; PMLS [= Areal des posteromedialen Sulcus lateralis suprasylvius]) unter wechselnden Reizbedingungen bilden dabei die Basis. Es wird deutlich, daß in allen Gebieten Neurone liegen, die auf sehr komplexe Reize reagieren. Dabei kommt der Objekt-Hintergrund-Interaktion eine große Bedeutung zu. Das Antwortverhalten der untersuchten Neurone ist sehr variabel. Dinse gelingt es aber, diese Variabilität durch neu eingeführte Aktivitätsmaße zu systematisieren und so ihren Informationsgehalt zu erkennen. Eine arealgebundene Aufgabenteilung wird deutlich, indem in den Areae 17 und 18 Formerkennung vorgefunden wird, während im PMLS-Areal Bewegungsverarbeitung lokalisiert ist.

Dinse legt eine wichtige Studie vor, die an dem Weg arbeitet, solche Hirnregionen zu verstehen, deren Komplexität sich dem einfachen Zugang entziehen. Sie zeigt, daß es möglich ist, hier Fortschritte zu erzielen. Zugleich wird in der Arbeit aber auch deutlich, wie schwierig der adäquate methodische Zugang ist. So provoziert der Beitrag letztlich auch die Frage, wie stark die beschriebenen Besonderheiten der visuellen Informationsverarbeitung auch von anderen Sinnesmodalitäten und dem Zustand der Hirnrinde überhaupt (Stichwort: ubiquitär in den Neocortex projizierende Transmittersysteme) beeinflußt werden.

Wenn auch eines der sehr ehrgeizigen Themen dieser Arbeit – der „Gegensatz zwischen lokalen Verarbeitungsstrukturen und globaler Wahrnehmung" – vielleicht noch nicht ganz abgehandelt ist, so ist herauszuheben, daß Dinse besonders zur Definition des „rezeptiven Feldes" – ein anderes Thema der Arbeit – Tore aufgestoßen hat, die eine Ausweitung des Begriffes nahelegen. Insgesamt wird dieses sehr spezielle Buch vor allem im Bereich der Neurobiologie auf einen großen Interessentenkreis stoßen.

G. Rehkämper, Köln

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